

Integrative taxonomy uncovers hidden diversity in Romanian *Geophilus* Leach, 1814 (Geophilomorpha, Geophilidae)

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Abstract

Two new species of *Geophilus* Leach, 1814, are identified and described from Romania. The examined material is compared with morphologically similar congeners, suggesting the presence of a complex of closely related species within the highly diverse genus *Geophilus*, characterized by a unique combination of diagnostic morphological and molecular characters. Two nuclear (18S, 28S) and one mitochondrial (COI) markers are sequenced for *Geophilus tenuis* **sp. nov.**, and COI sequence data are provided for *Geophilus captiosus* **sp. nov.** Morphological data, phylogenetic reconstruction, and three molecular species delimitation tools (ASAP, bPTP, and GMYC) confirm their validity, with diagnostic nucleotide combinations, based on the COI barcode, additionally provided for them. Their placement in *Geophilus* is assessed through the most complete phylogeny of the genus hitherto constructed, using sequence data of 18S, 28S, and COI markers from all species present in public repositories. The extent of potential undescribed species diversity in *Geophilus* is discussed, highlighting the need for comprehensive sampling of small endogeic members of this genus.

Key Words

Centipedes, molecular diagnosis, Southeast Europe, species delimitation, systematics

Introduction

The soil centipede genus *Geophilus* Leach, 1814, comprises ca. 140 species with a primarily Holarctic global distribution (Bonato 2011). Being the earliest described geophilomorph genus (Linnaeus 1758; Fourcroy 1785; Leach 1814), many soil centipede species described prior to the 20th century (e.g., Koch 1835; Gervais 1837; Pocock 1891; Silvestri 1895; Verhoeff 1898) were indiscriminately assigned to it due to a previously broader generic diagnosis. Subsequent taxonomic revisions of *Geophilus* (Attems 1929; Bonato and Minelli 2014) have allowed many of these incorrectly assigned species to be transferred to other genera and families (Pereira 2008; Bonato et al. 2011), clarifying their true status. Nevertheless, lack of a global generic revision of *Geophilus* presents a significant challenge to the resolution of intergeneric and

interfamilial relationships within the order Geophilomorpha (Bonato et al. 2014a).

Morphological characters shared by some groups of *Geophilus* species (e.g., the elongation of the antennae (Newport 1843), the reduction of the second maxillary pretarsus (Attems 1895; Verhoeff 1928), the apparent indistinctness of separations between labral pieces (Chamberlin 1912), or the presence of well-developed carpophagus structures (Verhoeff 1925)) have previously been used for justification of generic or subgeneric divisions. These proposed splits have been rejected in subsequent taxonomic reviews of *Geophilus* (Gervais 1847; Attems 1903; Crabill 1953; Minelli 1978; Bonato and Minelli 2014). However, the lack of molecular data for most species in the genus has hindered attempts to resolve outstanding taxonomic questions about their true affinities using an integrative approach (Bonato and Minelli 2009).

Past investigations of geophilomorph phylogenetic relationships failed to recover the monophyly of *Geophilus* using molecular, morphological, and total-evidence data (Bonato et al. 2014a), highlighting the challenge posed by its extensive morphological variability.

In Romania, eight *Geophilus* species are included in the most recent catalog of Geophilomorpha (Ion 2016), with one being described subsequently (Baba et al. 2024). Two of these, *Geophilus promontorii* Verhoeff, 1928, and *Geophilus proximus* C. L. Koch, 1847, are considered doubtful records that may refer to other *Geophilus* species (*Geophilus impressus* C. L. Koch, 1847, *Geophilus flavus* De Geer, 1778), as no subsequently collected specimens could reliably confirm the true identity of the records (Ion 2016). Predominantly, the species of *Geophilus* recorded from Romania have wide distributions across Europe (*Geophilus electricus* Linnaeus, 1758, *G. impressus*) or Central Europe (*Geophilus oligopus* Attems, 1895, *Geophilus pygmaeus* Latzel, 1880) (Ion 2016), with only one suggested as a narrow-range endemic restricted to the karst of the Dobrogean plateau, *Geophilus zagreus* Baba and Giurginca, 2024 (in Baba et al. 2024). Recent descriptions of small-sized geophilomorph species from other Southeastern European localities (Stojanović et al. 2019, 2024) suggest the current understanding of *Geophilus* diversity within Romania likely underestimates the number of species, considering the lack of coordinated sampling at the national scale (Baba et al. 2019).

We describe two new species, *Geophilus captiosus* sp. nov. and *Geophilus tenuis* sp. nov., from Romania. Using an integrative taxonomy approach, we find that in spite of differences in ecology and the distance between the type localities, they are closely related and part of a monophyletic group that includes the morphologically similar *G. flavus* and *G. zagreus*. Additionally, we employ three molecular species delimitation tools and a molecular diagnosis method to explore the extent of possible cryptic species diversity using publicly available and presently obtained *Geophilus* COI barcode data. To evaluate the relationships of the two new species to each other and other congeners, we construct a molecular phylogeny of *Geophilus* using three loci (nuclear ribosomal markers 18S and 28S and mitochondrial marker COI), including all species for which sequence data is available.

Materials and methods

Examined specimens

All specimens were hand-collected and stored in 70% ethanol. Type material of the new species was accessioned and deposited in the collection of the “Grigore Antipa” National Museum of Natural History. Examined non-type material belongs to the following collections: GP – George Popovici (personal collection), PD – Bonato–Minelli collection, Department of Biology, Università degli Studi di Padova, NHM – Natural History Museum (London).

The following specimens have additionally been examined:

Geophilus flavus De Geer, 1778

Romania • 10♀♀♂♂, (GP), Ilfov County, Voluntari (44.5190°N, 26.1332°E), ca. 90 m asl., oak and hornbeam forest, upper soil layers, 28 March 2021, leg. G. Popovici; • 2♀♀, same collection data as preceding, 11 April 2021.

Geophilus serbicus Stojanović, Mitić & Antić, 2019 (in Stojanović et al. 2019)

Serbia • 1♀, specimen number BZ11 (GP), Stara Planina Mts., Babin Zub (43.3737°N, 22.6133°E), ca. 1580 m a.s.l., old *Fagus moesiace montanum* forest, under stone, 15 June 2016, leg. D. Stojanović, D. Antić, S. Makarov; • 1♂, specimen number GBZ5 (GP), same collection data as preceding, 9 August 2021, leg. D. Stojanović, J. Milovanović, Z. Jovanović, V. Vujić; • 1♀, specimen number GBZ8 (GP), same collection data as preceding, 10 August 2021, e.g., D. Stojanović, J. Milovanović, Z. Jovanović, V. Vujić; • 1♂, specimen number GBZ10 (GP), COI molecular voucher (GenBank accession: [PZ130024](#)), same collection data as preceding.

Geophilus seurati Brolemann, 1924

Algeria • 3♀♀, (PD), Tala Tazouport, 11 May 1983.

Geophilus osquidatum

Italy • 2♀♀, 1♂, (PD), Genova Voltri, 19 March 1981, leg. Gardini.

Morphological data

Specimens were prepared for microscopy using protocols outlined by Pereira (2000). Dissection was carried out using a Leica M80 stereomicroscope, and specimens were examined using an Olympus CX21 light microscope. Figures were prepared with a drawing tube. Terminology for external morphology follows Bonato et al. (2010), except for terminology referring to the antennal sensilla, which follows Ernst (2000) and Pereira (2017). To aid identification, external morphology was compared between the two new species and other congeners (Table 1) by drawing from both literature data and direct examination of specimens listed in this manuscript. The other species of *Geophilus* evaluated and the sources of information on morphological data, compiled from *ChiloKey* (Bonato et al. 2014b) and recent publications, are listed below:

G. flavus: Berlese 1903 (as *Geophilus longicornis*); Attems 1928 (as *Pachymerium tristanicum*), 1929 (as *Geophilus longicornis*); Brölemann 1930 (as *Necrophloeophagus longicornis*); Eason 1964 (as

- Necrophloeophagus longicornis*); Matic 1972 (as *Necrophloeophagus longicornis*); Misiach 1978 (as *Necrophloeophagus longicornis*); Christian 1996; Andersson et al. 2005; Barber 2009; Simaiakis et al. 2010; Simaiakis et al. 2013.
- G. osquidatum*: Brölemann 1909, 1930; Verhoeff 1928 (as *G. scillyensis*); Turk 1947 (as *G. scillyensis*); Blower 1961; Eason 1964; Salinas 1990; Barber 2009.
- G. proximus*: Latzel 1880; Attems 1901 (as *G. ganonotus*), 1929 (as *G. commutatus* and *G. ganonotus*); Chalande 1909; Brölemann 1930; Hammer 1931; Lignau, 1933 (as *G. eremophilus*); Jawlowski 1949; Palmén 1949; Demange 1959; Enghoff 1971; Matic 1972; Kaczmarek 1979; Zaleskaja et al. 1982; Barber & Jones 1999; Andersson et al. 2005; Bonato et al. 2005; Barber 2009.
- G. pusillifrater*: Verhoeff 1898; Lewis 1961; Eason 1964; Iorio 2006; Barber 2009; Stojanović et al. 2019.
- G. pygmaeus*: Latzel 1880; Verhoeff 1895, 1896, 1898, 1934 (as *G. larii*), 1938, 1940; Silvestri 1896 (as *G. cispadanus*); Attems 1929; Peretti & Bonato 2016.
- G. serbicus*: Stojanović et al. 2019.
- G. seurati*: Meinert 1870 (as *G. gracilis*); Brölemann 1924; Attems 1929 (as *G. gracilis*); Iorio 2006 (as *G. gracilis*); Barber 2009 (as *G. gracilis*).
- G. zagreus*: Baba et al. 2024.

These species were chosen for comparison on the basis of similarities in the morphology of the forcipules and clypeus (*G. flavus*, *G. osquidatum*, *G. proximus*, *G. seurati*, and *G. zagreus*) or in the number of leg-bearing segments and body size (*G. pusillifrater*, *G. pygmaeus*, and *G. serbicus*) to the two new species, as determined using ChiloKey.

DNA extraction, amplification, and sequencing

Genomic DNA was extracted from *G. captiosus* sp. nov., *G. serbicus*, and *G. tenuis* sp. nov. (specimens used as molecular vouchers indicated in Suppl. material 1) using the Isolate II Genomic DNA Kit (Bioline, London, UK), following manufacturer specifications. A partial COI fragment was amplified using the universal PCR primers LCO1490 and HCO2198 (Folmer et al. 1994). The nuclear ribosomal genes 18S and 28S were amplified with 18sai–18sbi and RD1A–RD1B primer pairs, respectively, developed by Whiting (2002).

The PCR reactions were performed in a total volume of 50 µL containing 10 ng of DNA template, 1× Green GoTaq® Flexi Buffer, 2.5 mM MgCl₂, each dNTP at 0.1 mM, 0.5 µM of each primer, and 1.5 units of GoTaq® DNA polymerase (Promega, Madison, WI, USA). The PCR products were isolated from samples presenting clean and visible bands on a 0.5 µg ml⁻¹ ethidium bromide-stained agarose gel, using the Geneaid Gel/PCR Purification Kit (Geneaid Biotech Ltd., Taiwan), following manufacturer specifications. DNA sequencing was performed by Macrogen (Seoul, Korea). The resulting

sequences for the three genes were edited and aligned in CodonCode Aligner version 3.7.1 (CodonCode Corporation, Dedham, MA, USA).

Phylogenetic analysis

Phylogenetic relationships among *Geophilus* species were evaluated using publicly available sequence data and the new sequences presented in this manuscript. A range of outgroup taxa across Geophilomorpha (indicated in Suppl. material 1) was selected. As higher-level relationships within Geophilidae remain unresolved, every geophilid species for which 18S, 28S, and COI sequence data were available was included in the analysis.

COI, 18S, and 28S sequences for other *Geophilus* species were retrieved from GenBank (Suppl. material 1). Alignment of COI sequences was carried out in MEGAX (Kumar et al. 2018), using the MUSCLE algorithm, producing a final alignment length of 653 bp. The 18S and 28S ribosomal RNA fragments were aligned in MAFFT v.7 with the Q–INS–i specification (Kuraku et al. 2013; Katoh et al. 2019), accounting for RNA secondary structure. Sequences were trimmed in GBlocks v.0.91.1 (Castresana 2000; Talavera and Castresana 2007) and manually to keep only conserved regions, producing a final alignment length of 890 bp (18S) and 1099 bp (28S). Models of molecular evolution for each gene were selected in ModelFinder v.2.2.0 (Kalyaanamoorthy et al. 2017) based on the Akaike Information Criterion using the IQ-TREE and BEAST2 specifications, respectively (Table 1). Maximum likelihood (ML) phylogenetic trees were inferred using IQ-TREE v.2.2.0 (Nguyen et al. 2015) under the edge-unlinked partition model for 10,000 ultra-fast bootstraps (Minh et al. 2013), as well as the Shimodaira–Hasegawa-like approximate likelihood-ratio test (Guindon et al. 2010). Bayesian inference (BI) trees were estimated using BEAST v.2.7.8 (Bouckaert et al. 2019). All loci were analyzed with linked tree and unlinked clock models. A GTR model with gamma rates and an estimated proportion of invariant sites was specified for each locus, and an optimized relaxed clock model was specified for all three loci. Two independent MCMC runs of 50,000,000 generations, sampling trees every 1,000 generations, were conducted. Combined log files were analyzed in Tracer v.1.7.2 (Rambaut et al. 2018), ensuring all parameter ESS values exceeded 200. Tree files from both runs were combined in TreeAnnotator v.2.7.7 (Drummond and Rambaut 2007) with 10% of sampled trees discarded as burn-in.

Molecular species delimitation

Uncorrected *p*-distances for the *Geophilus* COI dataset were calculated in MEGA11 (Tamura et al. 2021) (Suppl. material 2).

Four DNA-based taxonomy methods (ASAP, bPTP, GMYC, and MOLD) were carried out on COI sequence

Table 1. Morphology of evaluated *Geophilus* in comparison with the two newly described species.

Character	Species				
	<i>G. captiosus</i>	<i>G. tenuis</i>	<i>G. flavus</i>	<i>G. osquidatum</i>	<i>G. proximus</i>
Adult body length (mm)	18–24	10–13	20–45	16–30	25–40
Leg-bearing segments	45–47	43–47	37–61	51–63	45–55
Ratio of length of antenna to cephalic plate length	ca. 4.5	ca. 3.6	ca. 4.1	ca. 4.6	ca. 2.5
Length to width ratio of cephalic plate	ca. 1.25	ca. 1.18	ca. 1.2	ca. 1.11	ca. 1.2
Clypeal areas	2	2	1	2	1–2
First maxillae lappets	Present	Present	Present	Present	Present
Tarsungulum protruding over anterior margin of cephalic plate	Yes	Yes	Yes	Yes	No
Forcipular tarsungulum basal tooth	Present	Present	Present	Present	Present
Armature of forcipular articles	Small sensillum coeloconicum on internal side of each article	Small sensillum coeloconicum on internal side of each article	Small sensillum coeloconicum on internal side of each article	Small sensillum coeloconicum on internal side of each article	No denticles or tubercles
Forcipular tarsungulum inner margin	Smooth	Smooth	Fine, irregular serrations	Large, regular serrations	Smooth
Chitin lines	Vanishing before reaching the condyles	Vanishing before reaching the condyles	Vanishing before reaching the condyles	Vanishing before reaching the condyles	Vanishing before reaching the condyles
Labrum medial part	7–8 tubercles	4–6 tubercles	6–8 tubercles	2 tubercles	1–4 tubercles
Carpophagus structures	Present on sternites 2–15; unconsolidated	Present on sternites 2–12; unconsolidated	Absent	Present on sternites 2–14	Present
Anterior sternites pore fields	Triangular; present on 1–15	Triangular; present on 1–15	Triangular; present on 1–15	Triangular; present on 1–15	Triangular; present on 1–17
Posterior sternites pore fields	Two small; present on 17 to penultimate	Two small; present on 16 to penultimate	Two small; present on 16 to penultimate	Two small. Present on 16 to penultimate	Absent
Isolated coxal pore	Present, same size as others	Present, reduced in size	Absent	Absent	Absent
Coxal pores	3–6, opening over entire ventral surface of coxopleuron	2–3, opening near margin of metasternite	2–10, opening near margin of metasternite	2–4, opening near margin of metasternite	8–10; opening near margin of metasternite
Anal pores	Present	Present	Present	Present	Present
Ultimate pleuropretergite entire	Yes	Yes	Yes	Yes	Yes
Ultimate leg pair pretarsus	Evident, claw-shaped	Evident, claw-shaped	Reduced in size, claw-shaped	Reduced in size, claw-shaped	Evident, claw-shaped
Adult body length (mm)	11.5–13	Max. 20	16.6–18	34–36	30–63.9
Leg-bearing segments	39–43	41–47	41–45	55–63	51–53
Ratio of length of antenna to cephalic plate length	ca. 3.4	ca. 2	ca. 3.5	ca. 5.6	ca. 4.5
Length to width ratio of cephalic plate	ca. 1.3	ca. 1.1	ca. 1.11–1.18	ca. 1	ca. 1.05
Clypeal areas	0	0	0	2	2
First maxillae lappets	Absent	Present	Present	Present	Present
Tarsungulum protruding over anterior margin of cephalic plate	Yes	Yes	Yes	Yes	Yes
Forcipular tarsungulum basal tooth	Present	Present	Present	Present, occasionally reduced to shallow bulge only	Present
Armature of forcipular articles	-	Shallow bulge on intermediate articles	Small sensillum coeloconicum on internal side of each article	Small sensillum coeloconicum on internal side of each article	Small sensillum coeloconicum on internal side of each article
Forcipular tarsungulum inner margin	Smooth	Smooth	Smooth	Large, regular serrations	Smooth
Chitin lines	“Evident”; vanishing before reaching the condyles	Vanishing before reaching the condyles	Vanishing before reaching the condyles	Vanishing before reaching the condyles	Vanishing before reaching the condyles
Labrum medial part	-	2 tubercles	8 tubercles	5–6 tubercles	3 tubercles
Carpophagus structures	Absent	Present on sternites 2 – 13	Small median plateau on some anterior sternites	Present	Present on sternites 1–16; unconsolidated
Anterior sternites pore fields	Band-shaped; present on 1–11	Band-shaped; present on 1–14	Sub-triangular; present on 1–12(13)	Triangular; present on 1–15	Triangular; present on sternites 1–18(19)(20)
Posterior sternites pore fields	Two small; present only on 12–18	Small clusters of few pores	Two small; present on 13-14 to penultimate	Two small; present on 16 to penultimate	Two small; present on 18(19)(20) to penultimate
Isolated coxal pore	Present, reduced in size	Present, reduced in size; in middle of coxopleuron	Present, same size as others	Absent	Present, same size or larger

Character	Species				
	<i>G. captiosus</i>	<i>G. tenuis</i>	<i>G. flavus</i>	<i>G. osquidatum</i>	<i>G. proximus</i>
Coxal pores	ca. 3–5, opening near margin of metasternite	3–4, opening near margin of metasternite, one at anterior tip	3–7, opening over entire ventral surface of the coxopleuron	3–5, opening near margin of metasternite	9–18, opening over entire ventral surface of coxopleuron
Anal pores	Present	Present	Present	Present	Present
Ultimate pleuropretergite entire	-	Yes	Yes	Yes	Yes
Ultimate leg pair pretarsus	Claw-shaped in female; reduced to tubercle in male	Evident, claw-shaped	Evident, claw-shaped	Reduced in size, claw-shaped	Evident, claw-shaped

data to evaluate cryptic diversity within *Geophilus* and assess congruence between identified morphospecies and candidate species suggested by molecular data.

Assemble Species by Automatic Partitioning (ASAP) (Puillandre et al. 2021) was carried out via a locally compiled GUI version of the program ASAPy 1.0 downloaded from the iTaxotools website to partition the 658 bp COI dataset into putative species following a hierarchical clustering algorithm relying on pairwise genetic distances. The robustness of ASAP delimitation is supported by two ranking systems, ranking both the p-value of partitions in ascending order and the relative width of the barcode gap in descending order. The final ASAP score is taken as the mean of the two ranks, the lowest indicating the favored partition. The Kimura-2-parameter distance method was specified, with a default transition/transversion rate of 2.0. All other parameters were maintained with default settings.

The general mixed yule–coalescent model (GMYC) (Fujisawa and Barraclough 2013), as implemented on the web-based server (<https://species.h-its.org/gmyc/>), was applied to identify shifts in branching rates along an ultrametric phylogenetic tree coinciding with the transition from intra- to interspecific branching, indicating a species boundary. The threshold parameter was maintained at its default value (single threshold).

The Poisson Tree Processes (PTP) model was employed for species delimitation based on non-ultrametric rooted phylogenies through the online platform bPTP server: a Bayesian implementation of the PTP model for species delimitation (<https://species.h-its.org/ptp/>). In contrast to GMYC, PTP directly uses the number of substitutions to delimit species (under the assumption that this will be higher inter- than intraspecifically), without using time to identify branching rate transition points (Zhang et al. 2013).

MOLD (MOlecular Diagnoses) identifies diagnostic nucleotide combinations (DNCs) in DNA sequence alignments for the taxa of interest, enabling formal diagnosis based on sequence data (Fedosov et al. 2022). To improve reliability of molecular description, MOLD introduces a type of DNA diagnosis, “redundant DNC” (rDNC), which considers unsampled genetic diversity. MOLD was used for molecular diagnosis of all species of *Geophilus* in the present dataset under the following parameters: gaps treated as missing data, cutoff: 100, number of iterations: 10,000, maximum length of raw mDNCs: 12, maximum length of refined mDNCs: 7, simulated sequences up to 1.0 percent divergent from original ones, maximum

number of sequences modified per clade: 5, and a scoring threshold for the rDNCs in two consecutive runs of 95.

Ecological data

Where available, information on the habitat where the specimens have been collected is provided. Local vegetation assemblages are classified according to Doniță et al. (1992). A map of the type localities of the two new species, as well as *G. zagreus* and *G. serbicus*, was constructed in QGIS v.3.40.5 using Google Maps satellite layer (Map Data 2025 © Google) as a base map. Occurrence records for voucher specimens of the two new species described are additionally provided in Darwin Core format (Wieczorek et al. 2012) (Suppl. material 3).

Results

Class Chilopoda Latreille, 1817
Order Geophilomorpha Pocock, 1896
Family Geophilidae Leach, 1815

Genus *Geophilus* Leach, 1814

Type species. *Geophilus electricus* Linnaeus, 1758

Geophilus captiosus Popovici, Popa & Iorgu, sp. nov.

Material examined. Holotype. Romania • ♀ (MNIN-GA CHI103), Hunedoara County, Gura Apelor, Retezat National Park (45.3414°N, 22.7195°E), ca. 1080 m asl., mixed coniferous and deciduous forest, upper soil layers, 27 July 2020, leg. G. Popovici.

Paratypes. • 1♀ (MNINGA CHI106), same as holotype; • 3♂♂ (MNINGA CHI104, MNINGA CHI105, and MNINGA CHI107), same as holotype.

Other materials. Romania • 1♂ 5♀♀, (NHM NHMUK015991407), same as holotype.

Diagnosis. Characterized by the following unique combination of characters: 45–47 leg-bearing segments; antennae 4.5 longer than cephalic plate, articles II–VII elongate, 1.63–1.7 times longer than wide; cephalic plate length/width ratio > 1.2; clypeus with two evident clypeal areas; forcipular coxosternite as long as wide, with incomplete chitin lines; inner margin of forcipular tarsungulum without crenulation; metasternites 2–15

with unconsolidated carpophagus structures (*sensu* Crabill 1954) and spindle-shaped pore fields; posterior metasternites including the penultimate with two posterior clusters of pores; coxopleuron of last leg-bearing segment with coxal pores opening independently on entire ventro-lateral surface; telopodite of ultimate leg pair with claw-shaped pretarsus.

Description of examined material. *Habitus*: 45–47 leg-bearing segments, body length 18–24 mm, color of preserved specimens yellow, with darker head and forcipular segment.

Head and antennae (Fig. 1): Cephalic plate approximately 1.25 times longer than broad (0.61–0.65 mm long, 0.49–0.52 mm wide), with straight posterior margin overlapped by the forcipular tergite. Chaetotaxy illustrated in Fig. 1. Basal plate and sulci absent. Antennae approximately 4.5 times longer than the cephalic plate (2.7–2.9 mm long), with basal articles distinctly elongate (1.63–1.7 times longer than wide). Articles I–X with rows of 2–4 type a sensilla dorsally and laterally, articles XI–XIII with one type a sensillum dorsally. Article XIV approximately two times longer than wide, with two rows of sensilla basiconica laterally, occupying 20% of its length and a small cluster of type b sensilla apically.

Clypeus (Fig. 2A, B): Uniformly reticulated, with one or two clypeal areas circumscribing the intermediate pair of sensilla. Clypeal setation comprising three pairs of sensilla, the largest being the intermediate. Clypeal areas lighter than surrounding cuticle, with indistinct but visible reticulation. Paraclypeal sutures faintly curved.

Labrum (Fig. 2A): Intermediate part with 7–8 tubercles, of which the central 5 are most visible and strongly sclerotized. Lateral parts with 7–9 hyaline bristles.

Mandible: Typical geophilid aspect with fine reticulation and a single pectinate lamella.

First maxillae (Fig. 2C, E): Triangular coxosternal projections present; telopodites biarticulated, slightly longer than projections; coxosternal and telopodal lappets present and prominent, reaching just below the tip of the distal telopodal article.

Second maxillae (Fig. 2C, D): Coxosternite undivided, with widely concave anterior margin. Articles 1 and 2 with 1–3 sensilla coeloconica laterally; article 3 densely setose distally, terminating in a large, claw-shaped pretarsus bearing an evident distal pore.

Forcipular segment (Fig. 2F–H): Forcipular tergite narrowing anteriorly. Forcipular coxosternite approximately as broad as long (1.03 times wider than long), slightly broader than the cephalic shield, and visibly protruding over the anterior edges of the forcipular tergite. Chitin lines vanishing before reaching the condyles, pointing laterally to them. Anterior margin with a shallow but evident notch and without denticles. Isolated reticulation pattern and chaetotaxy as in Fig. 2F. Forcipules extending slightly past the anterior edge of the cephalic shield when closed. Forcipular trochanteroprefemur approximately 1.6 times longer than broad. Forcipular articles with evident sensillum coeloconicum on the internal

side but no denticles (Fig. 2H); tarsungulum moderately curved, with smooth internal margin. Denticle at the base of the tarsungulum conspicuous, with rounded apex. Calyx of venom gland ovoid to hemispheric in shape, located mostly in the femoroid (Fig. 2G).

Trunk (Fig. 3): Tergites wider than long, without grooves or sulci, indistinctly reticulated and moderately setose. Walking legs largely homonomous along the entire trunk. Pretarsus claw-shaped, basally armed with a small accessory spine. Presternites well-developed, divided along the entire trunk. Metasternites sub-trapezoidal. First metasternite with central cluster of pores (Fig. 3A). Second to penultimate metasternite with evident, well-developed pore fields. Anterior metasternites (2–15) with single, spindle-shaped pore field located in the posterior half. Carpophagus structures present on metasternites 2–15, poorly sclerotized but evident, with pits occupying approximately one third of the anterior metasternite edge and finely reticulated pegs present on the posterior metasternite edge. Posterior metasternites elongated, approximately 1.4–1.6 times longer than broad and with two small, approximately circular pore fields located in the posterior third.

Last leg-bearing segment (Fig. 4): Ultimate pleuropretergite complete. Ultimate metatergite 1.2 times broader than long, with gently curved, convex posterior margin. Ultimate metasternite trapezoidal, 1.4 (female) to 1.46 (male) times broader than long, with straight posterior margin. Coxopleurae moderately enlarged, with 3–6 coxal pores scattered on the ventral surface of the coxopleuron. One isolated pore opening posteriorly, of the same size as the other coxal pores. Telopodite gracile in female holotype (4.3 times longer than metasternite) and slightly swollen in male paratype (4.8 times longer than metasternite), more densely setose on the ventral side and ending with a strong, curved pretarsus with a small accessory spine.

Postpedal segments (Fig. 4): Female with weakly bilobed gonopodal lamina. Male with strongly setose biarticulate gonopods flanking the penis. Anal pores distinct, opening near the margin of the anal valves.

Etymology. Derived from the Latin term for “deceptive” (“captiosus”) due to its initial misidentification as a species of *Pachymerium* C. L. Koch, 1847, based on superficial morphological characters.

Remarks. *G. captiosus* sp. nov. most closely resembles *G. flavus*, *G. tenuis* sp. nov., and *G. zagreus* in external morphology, sharing with these three congeners the elongation of the proximal antennal articles, the presence of one or more clypeal areas, the presence of lappets on the first maxillae, incomplete chitin lines on the forcipular coxosternite, the presence of a denticle at the base of the forcipular tarsungulum, and tarsungula that conspicuously project over the anterior margin of the head (Table 1). It can be distinguished from *G. tenuis* sp. nov. by the greater elongation of the antennae relative to the cephalic plate (4.5 times longer than cephalic plate in *G. captiosus* sp. nov.; 3.6 times in *G. tenuis* sp. nov.) and

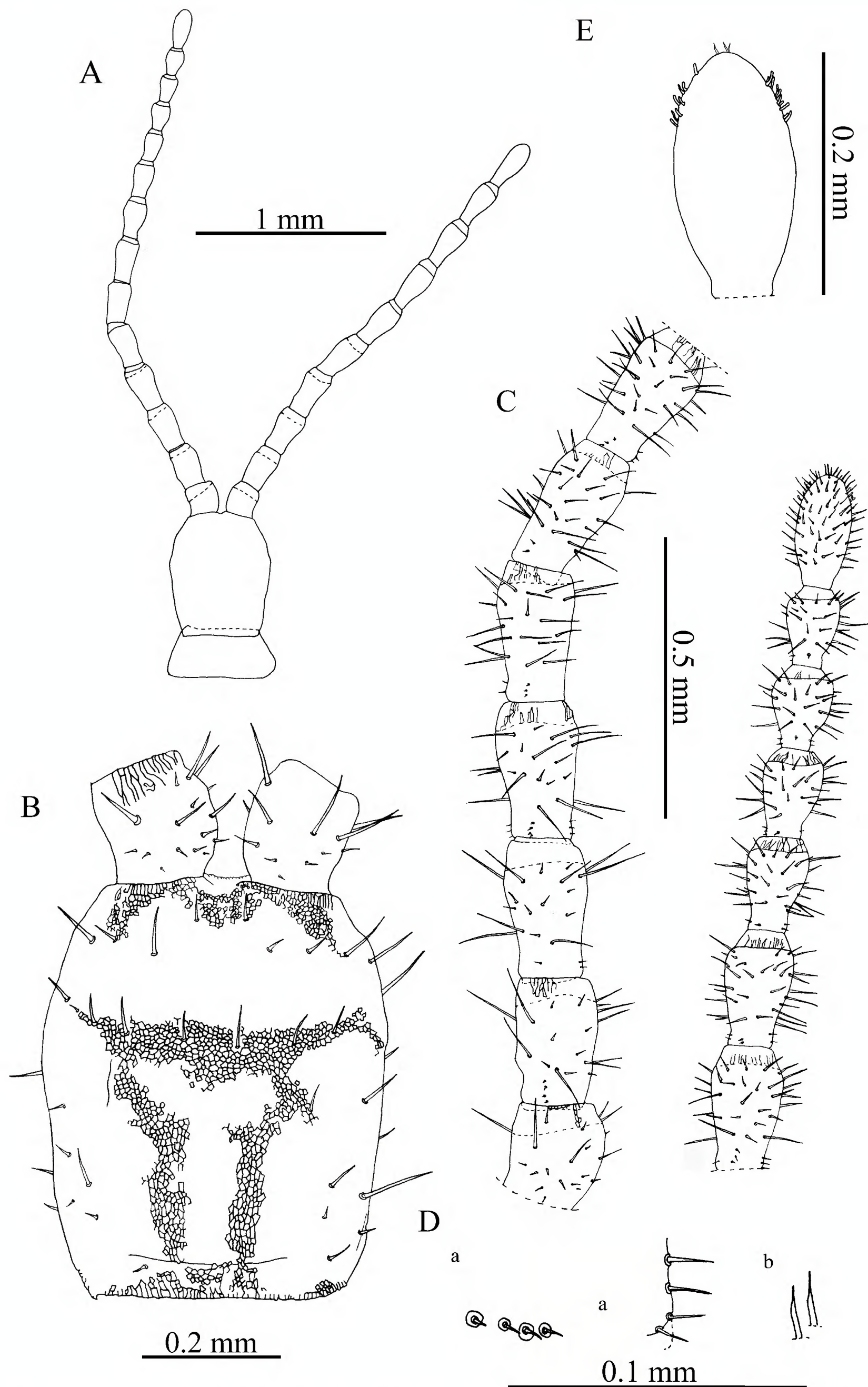


Figure 1. *Geophilus captiosus* sp. nov. holotype (female) **A.** Cephalic capsule and antennae, dorsal view (CHI103); **B.** Cephalic capsule, dorsal view (CHI103); **C.** Left antenna, dorsal view (CHI103); **D.** Type a and type b sensilla on antennae (CHI103); **E.** Antennal article XIV showing type b sensilla and sensilla basiconica (CHI103).

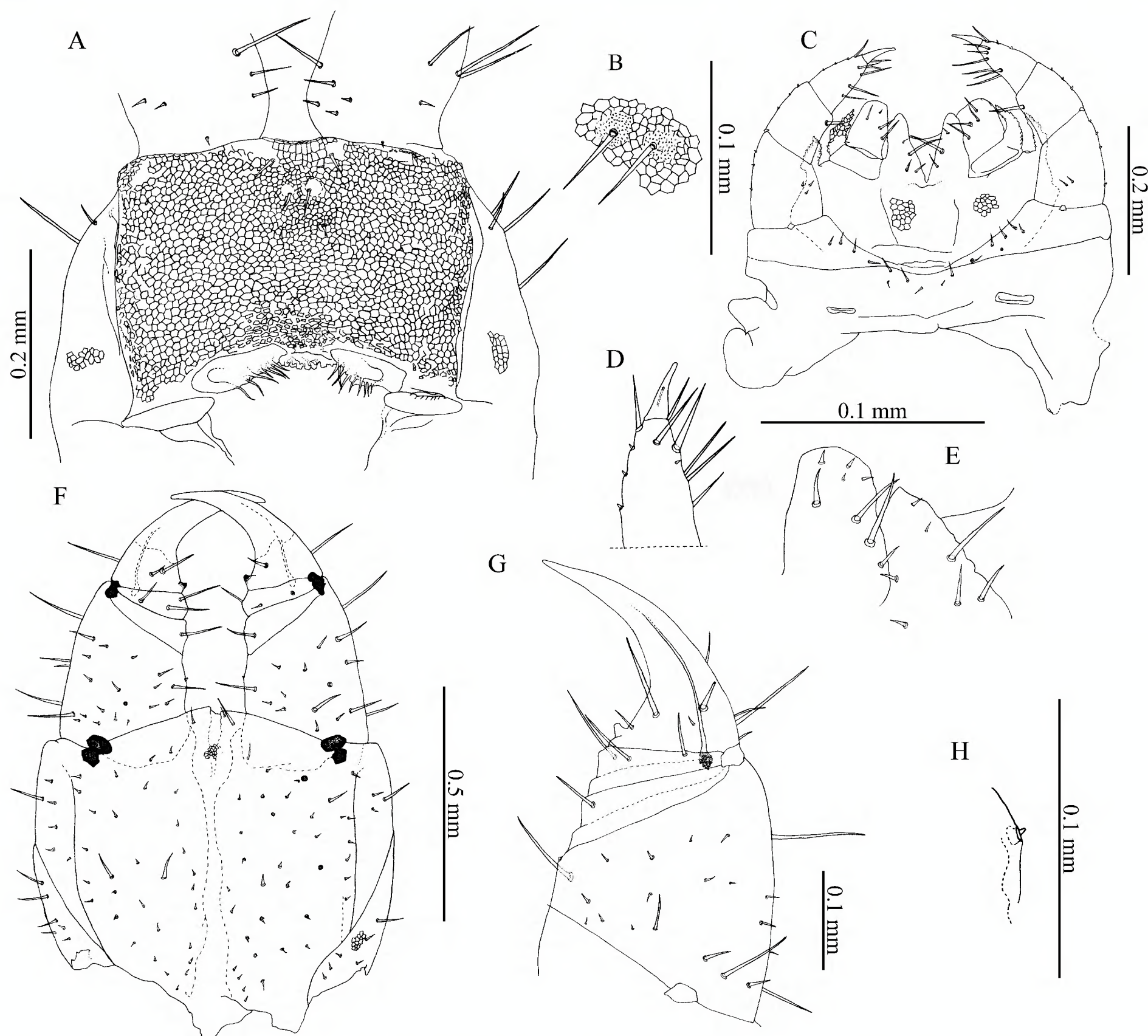


Figure 2. *Geophilus captiosus* sp. nov. **A.** Clypeus and labrum, ventral view (CHI103, holotype female); **B.** Clypeal areas, ventral view (CHI103, holotype female); **C.** Maxillae, ventral view (NHMUK015991407); **D.** Second maxilla article III and pretarsus, ventral view (NHMUK015991407); **E.** First maxilla telopodite and coxosternal projection, ventral view (NHMUK015991407); **F.** Forcipular coxosternite, ventral view (CHI103, holotype female); **G.** Right forcipule, ventral view (CHI103, holotype female); **H.** Sensillum coeloconicum on internal side of trochanteroprefemur, lateral view (CHI103, holotype female).

the arrangement of the coxal pores (scattered over entire ventro-lateral surface of coxopleuron in *G. captiosus* sp. nov.; opening near the edge of the metasternite in *G. tenuis* sp. nov.). It can be distinguished from *G. zagreus* by its smaller adult body size (< 25 mm in *G. captiosus* sp. nov.; 30–63 mm in *G. zagreus*), smaller number of leg-bearing segments (45–47 in *G. captiosus* sp. nov.; 51–53 in *G. zagreus*), more elongate cephalic plate (1.25 times longer than wide in *G. captiosus* sp. nov.; approximately as long as wide in *G. zagreus*), and greater number of tubercles on the mid-piece of the labrum (7–8 in *G. captiosus* sp. nov.; 3 in *G. zagreus*). Unlike *G. flavus*, *G. captiosus* sp. nov. does not have fine, irregular serrations on the internal edge of the tarsungulum or a reduced pretarsus on the ultimate leg telopodite. It can be additionally distinguished from *G. flavus* by the

presence of a conspicuous isolated coxal pore and the distribution of the coxal pores (opening near the edge of the metasternite only in *G. flavus*). *G. captiosus* sp. nov. differs from *G. pusillifrater* and *G. pygmaeus* in the presence of clypeal areas, which the latter two species lack; the elongation of the antennae (not elongate in *G. pygmaeus*); the presence of first maxillary lappets (absent in *G. pusillifrater*); the presence of carpophagus structures (absent in *G. pusillifrater*); and its characteristic coxal pore arrangement, which differs from both species (Table 1). *G. proximus* resembles *G. captiosus* sp. nov. in the elongation of the cephalic plate and the presence of clypeal areas but can be readily distinguished from it by the morphology of its carpophagus structures (strongly sclerotized and consolidated *sensu* Crabill (1954) in *G. proximus*; unconsolidated *sensu* Crabill 1954 in

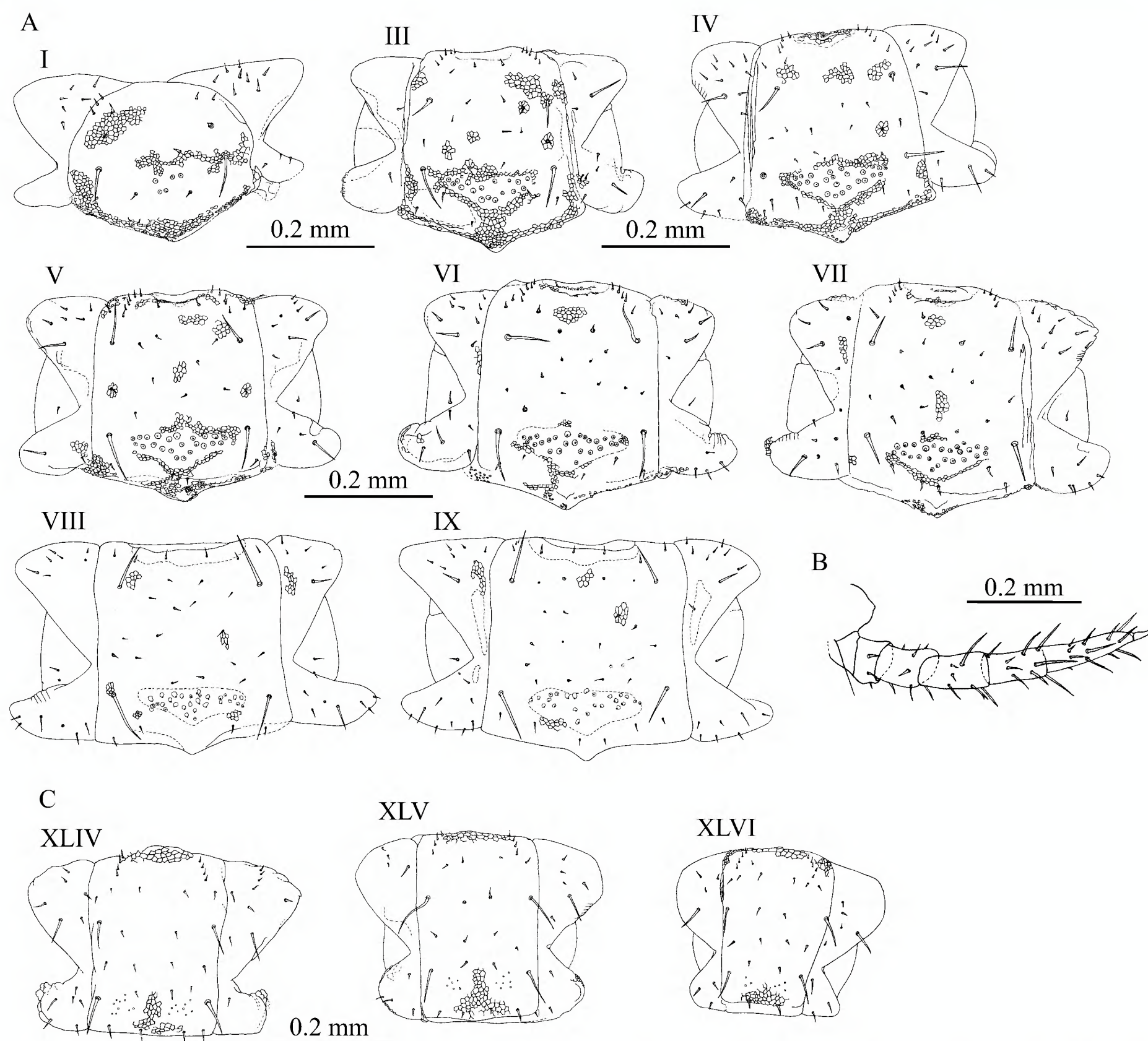


Figure 3. *Geophilus captiosus* sp. nov. **A.** Anterior sternites (I, III–IX), ventral view (CHI106); **B.** Walking leg 44, lateral view (CHI106); **C.** Posterior sternites (XLIV–XLVI), ventral view (CHI106).

G. captiosus sp. nov.), the elongation of its forcipules (tarsungula not protruding beyond the anterior margin of the head in *G. proximus*; protruding in *G. captiosus* sp. nov.), the absence of pore fields on the posterior trunk metasternites (present in *G. captiosus* sp. nov.), and the arrangement of the coxal organs. *G. osquidatum* and *G. seurati* similarly resemble *G. captiosus* sp. nov. in the presence of paired clypeal areas and the elongation of the antennae but can be readily distinguished from it by their characteristic, shared morphology of the last leg-pair pretarsus, which is reduced in size (conspicuous, not reduced in *G. captiosus* sp. nov.).

The arrangement of the coxal pores mirrors the condition of *G. serbicus*, a geographically proximate congener, which also resembles the two species here described in overall habitus (Stojanović et al. 2019). However, *G. serbicus* differs from *G. captiosus* sp. nov. in adult body length, number of leg-bearing segments, elongation of the antennae and cephalic capsule, clypeal morphology, and the arrangement of sternal pore fields (Table 1).

Geophilus tenuis Popovici, Popa & Iorgu, sp. nov.

Material examined. Holotype. Romania • ♀ (MN-INGA CHI108), Ilfov County, Voluntari (44.5244°N, 26.1141°E), ca. 100 m asl., oak and hornbeam forest, upper soil layers, 16 April 2021, leg. G. Popovici.

Paratypes. Romania • 1♂ (MNINGA CHI110), same as holotype, 23.05.2021; • 1♀ (MNINGA CHI111), Ilfov County, Voluntari (44.5191°N, 26.1332°E), ca. 90 m asl., 28 March 2021, leg. G. Popovici; • 1♀ (MN-INGA CHI112), same as preceding, 04.03.2022; • 1 juvenile (MNINGA CHI109), Ilfov County, Voluntari (44.5221°N, 26.0914°E), ca. 100 m asl., 30 May 2021, leg. G. Popovici.

Other materials. Romania • 17♂♂♀♀, (GP), same as holotype.

Diagnosis. Characterized by the following unique combination of characters: Small-sized *Geophilus* species (adult body length ≤13 mm); 43–47 leg-bearing segments; antennae 3.5–3.8 times longer than cephalic plate,

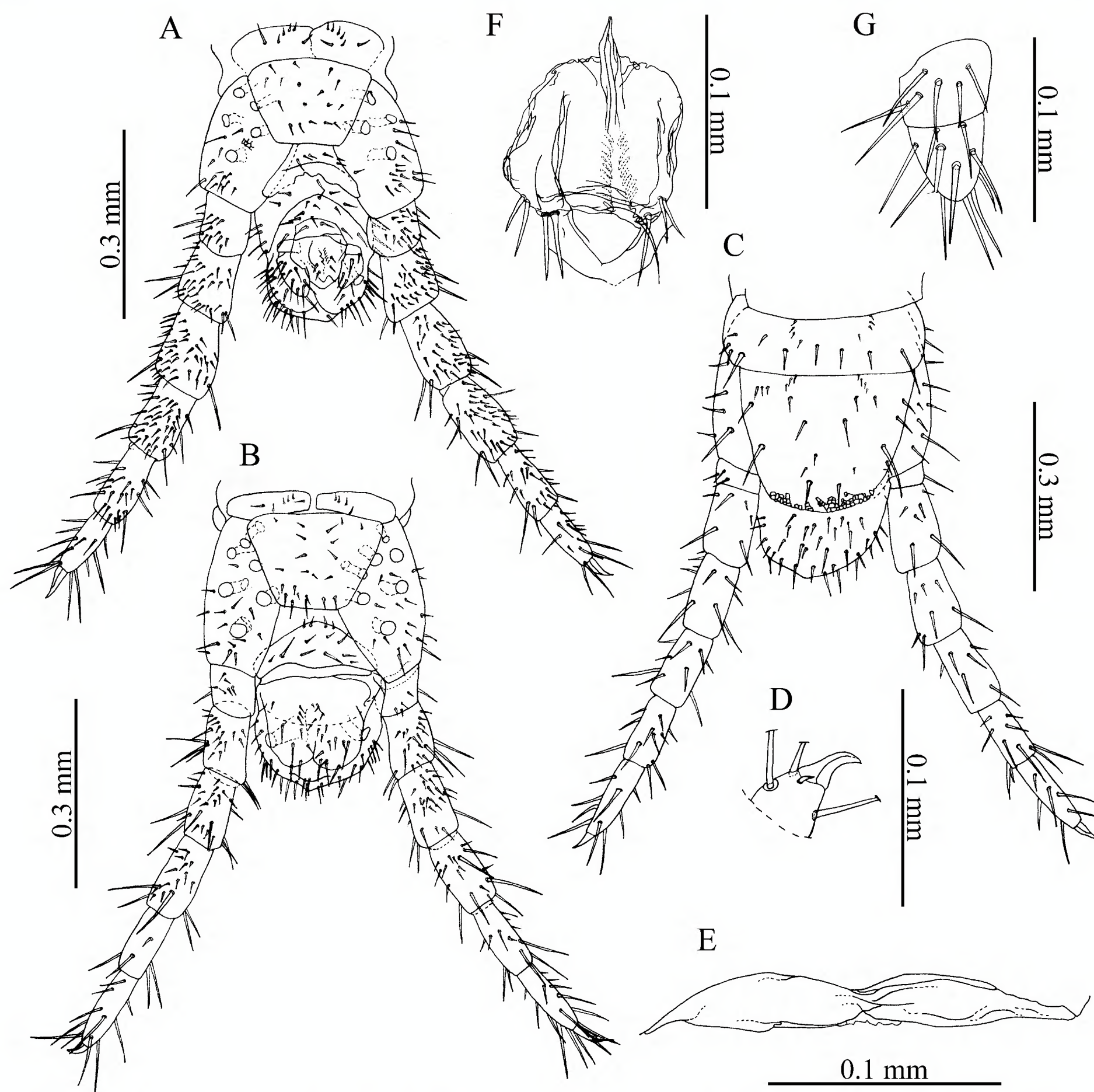


Figure 4. *Geophilus captiosus* sp. nov. **A.** Ultimate leg-bearing segment of male, ventral view (CHI105); **B.** Ultimate leg-bearing segment of female, ventral view (CHI103); **C.** Ultimate leg-bearing segment of female, dorsal view (CHI103); **D.** Ultimate leg pair pretarsus; **E.** Female gonopodal lamina, ventral view (CHI103); **F.** Male gonopod, ventral view (CHI105); **G.** Penis, ventral view (CHI105).

articles II–VII elongate, 1.6–1.74 times longer than wide; cephalic plate 1.18 times longer than broad; clypeus with two evident clypeal areas; forcipular coxosternite approximately as long as wide, with incomplete chitin lines; inner margin of forcipular tarsungulum without crenulation; metasternites 2–12 with unconsolidated (*sensu* Crabill 1954), faint carpophagus structures and spindle-shaped pore fields; posterior metasternites including the penultimate with two posterior clusters of pores; coxopleuron of last leg-bearing segment with coxal pores opening individually, near the edge of the metasternite, partially covered by it; one isolated coxal pore opening laterally to the others; telopodite of ultimate leg pair with claw-shaped pretarsus.

Description of examined material. *Habitus.* 43–47 leg-bearing segments in examined specimens. Body length 10–13 mm. Color of preserved specimens pale yellow with darker cephalic plate and forcipular segment.

Head and antennae (Fig. 5): Cephalic plate approximately 1.18 times longer than broad (0.58 mm long, 0.5 mm wide) with distinct dorsal reticulation, straight posterior margin and absent basal plate. No paramedian or other sulci. Chaetotaxy illustrated in Fig. 5B. Antennae 3.5–3.8 times longer than head (1.8–2.2 mm long) and distinctly elongate with basal antennal articles 1.6–1.74 times longer than wide. Dorsal chaetotaxy as in Fig. 5C. Articles I–IX with 2–3 type a sensilla basally, articles X–XIII with 1 type a sensillum basally (Fig. 5C). Article XIV with lateral groups of sensilla basiconica occupying

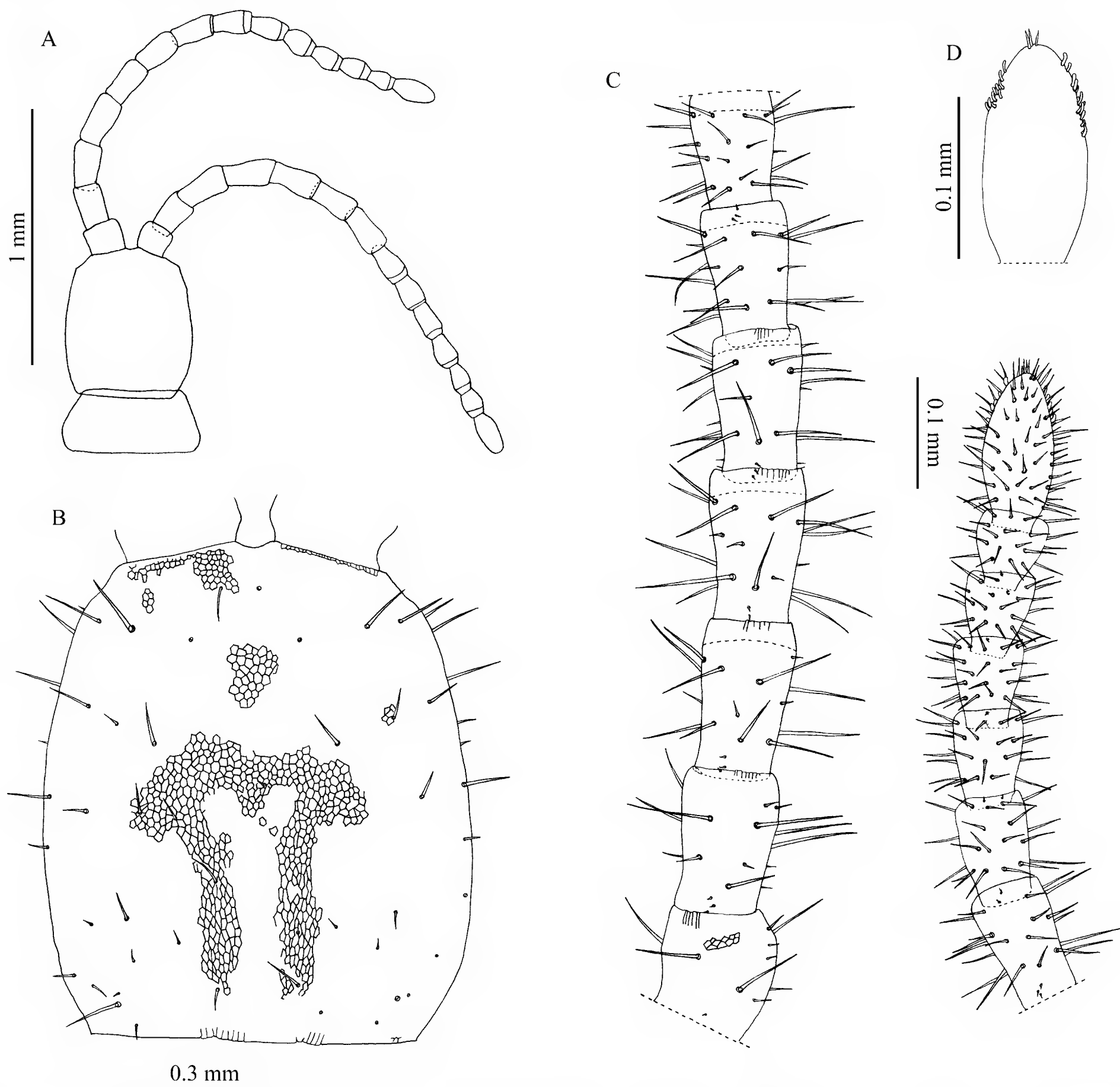


Figure 5. *Geophilus tenuis* sp. nov. **A.** Head and antennae, dorsal view (CHI108); **B.** Cephalic capsule, dorsal view (CHI108); **C.** Left antenna, dorsal view (CHI110); **D.** Antennal article XIV showing type b sensilla and sensilla basiconica (CHI110).

approximately 30% of its length and with a small cluster of type b sensilla at its distal apex (Fig. 5D).

Clypeus (Fig. 6A, B): Clypeus uniformly reticulated, with two evident clypeal areas. With three pairs of setae, the postantennal and posterior being smaller than the intermediate pair. (Fig. 6A). Clypeal areas lighter than surrounding cuticle, with indistinct but visible reticulation.

Labrum (Fig. 6A, B): Labrum with distinct lateral parts. Intermediate part with 5–6 tubercles, but only 2–3 visibly well-sclerotized in the center. Lateral parts with 5–7 hyaline filaments.

Mandible (Fig. 6E): One single pectinate lamella present on distal edge. Of a typical aspect for the genus.

First maxillae (Fig. 6C, D). Coxosternite entire. Distinct, sub-triangular coxal projections with 3–4 sensilla trichodea and 1–3 sensilla microtrichodea on their ventral

side. Coxosternal and telopodal lappets present, weakly developed (Fig. 6D). Articulation of telopodite indistinct.

Second maxillae (Fig. 6C, D). Coxosternite undivided, distinctly reticulated and with broadly concave anterior margin. Row of sensilla trichodea present medio-ventrally. Telopodite articles elongate (article I ca. 1.2, article II ca. 1.0, and article III ca. 1.7 times longer than wide) with distinct condyles and articulations. All articles with 1–3 sensilla coeloconica laterally. Pretarsus simple, claw-shaped with small pore opening distally (Fig. 6D).

Forcipular segment (Fig. 7): Forcipular tergite anteriorly narrowing, trapeziform. Forcipular coxosternite approximately as wide as long. Chitin lines vanishing before reaching the condyles, pointing laterally to them. Anterior margin with a shallow but evident notch and without denticles. Isolated reticulation pattern and chaetotaxy as in Fig. 7D. Forcípules extending slight-

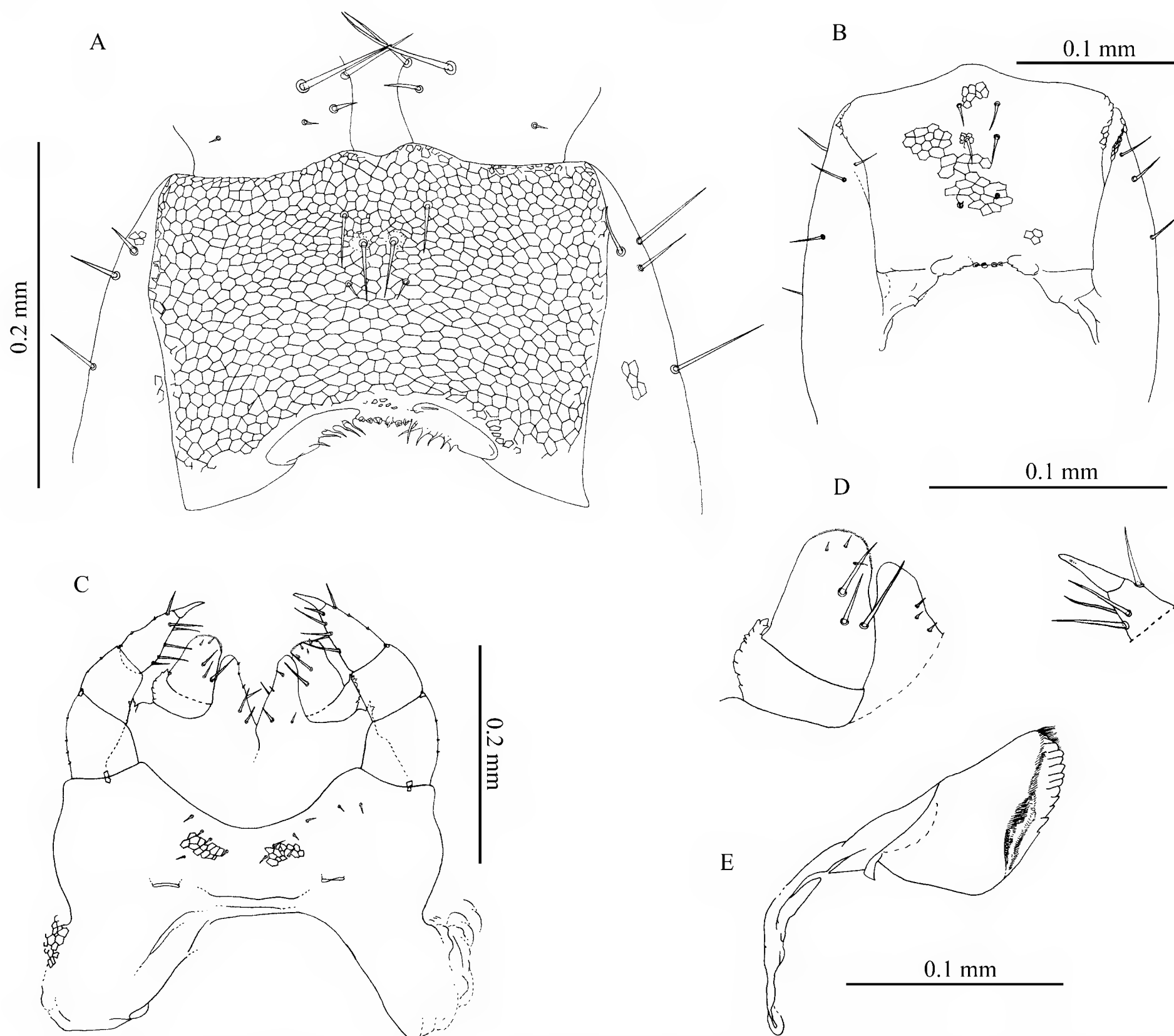


Figure 6. *Geophilus tenuis* sp. nov. **A.** Clypeus and labrum, ventral view (CHI108); **B.** Clypeus and labrum, juvenile, ventral view (CHI108); **C.** Maxillae, ventral view (CHI108); **D.** Maxillary telopodites, Maxilla I left, Maxilla II claw right, ventral view (CHI108); **E.** Mandible (CHI108).

ly past the anterior margin of the cephalic plate when closed. Forcipular trochanteroprefemur ca. 1.3 times longer than wide. Denticle at the base of tarsungulum conspicuous, straight, with rounded apex. Tarsungulum with smooth inner margin. All forcipular articles present a prominent sensillum coeloconicum on the internal side but no denticles (Fig. 7A, B). Calyx of venom gland oval, opening in femoroid (Fig. 7C).

Trunk (Fig. 8). Tergites wider than long, without grooves or sulci, indistinctly reticulated and moderately setose. Walking legs largely homonomous along the entire trunk (Fig. 8B). Pretarsus claw-shaped, basally armed with a small accessory spine. Presternites well-developed, divided along the entire trunk. Metasternites sub-trapezoidal. First metasternite with central cluster of pores (Fig. 8A). Pore fields present on all sternites excepting that of the ultimate leg-bearing segment. Anterior segments (2–15) with spindle-shaped, undivided pore fields. Carpophagus structures faint, present on sternites 2–12. Posterior metasternites elongate, 1.4–1.5 times longer

than broad, and with two small, approximately circular pore fields located in the posterior third. All sternites with two converging rows of sensilla trichodea anteriorly and two pairs of large sensilla trichodea laterally.

Last leg-bearing segment (Figs 9A, B, 10): Ultimate pleuropretergite complete. Ultimate metatergite 1.2 times wider than long. Ultimate metasternite trapezoidal, ca. 1.5 times wider than long, with straight posterior margin. Coxopleurae moderately enlarged, with 2–3 coxal organs opening close to the edge of the metasternite, partly covered by it, and one isolated posterior pore, reduced in size. Telopodite elongate in female holotype (4.1 times longer than metasternite), more densely setose on the ventral side and ending in a strong, curved pretarsus provided with a small accessory spine. Telopodite moderately swollen in male paratype (4.2 times longer than metasternite), more densely setose on ventral side.

Postpedal segments (Figs 9B, 10): Female with weakly bilobed gonopodal lamina (Fig. 9B). Male with penis flanked by two biarticulate, densely setose gonopods

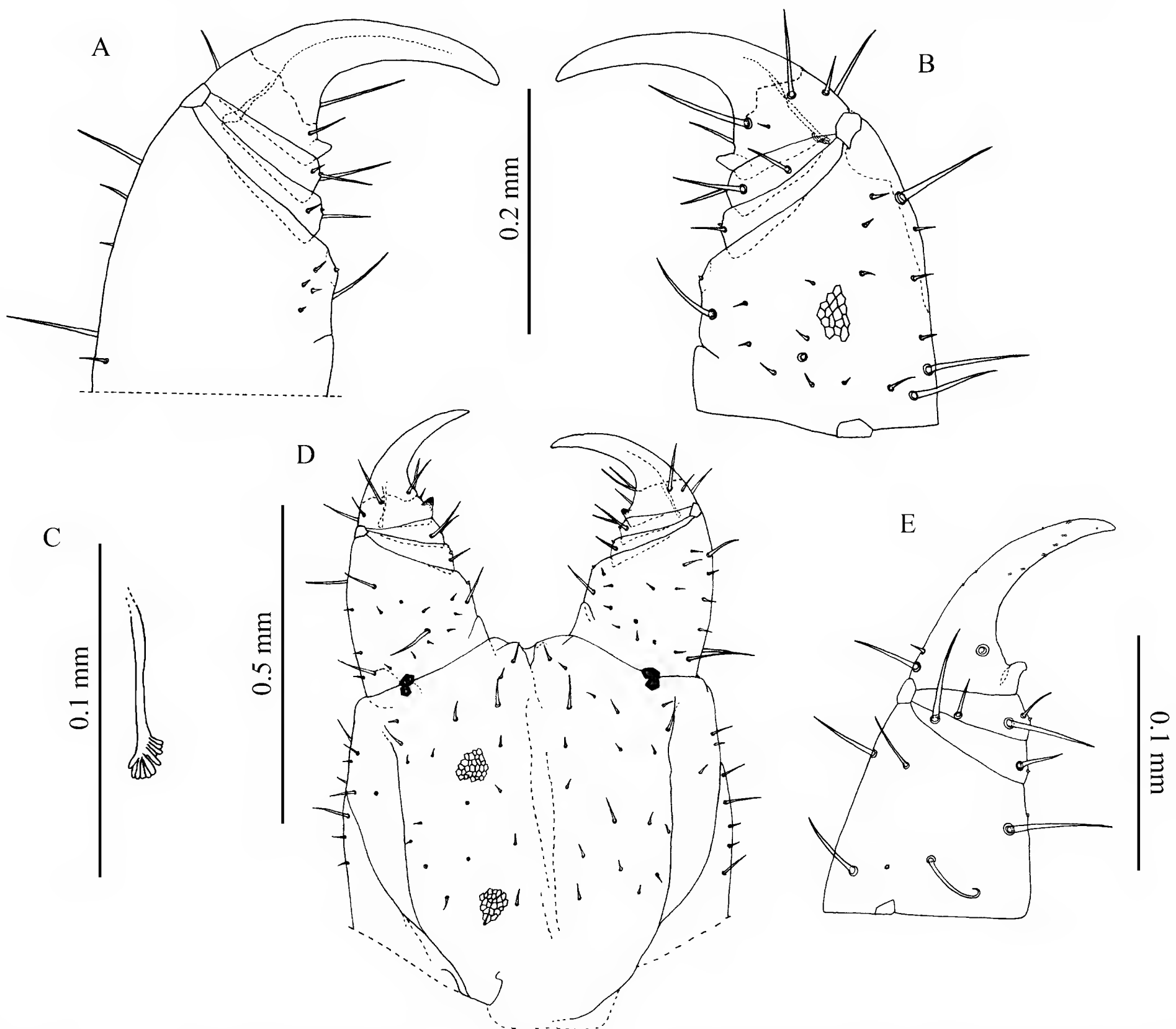


Figure 7. *Geophilus tenuis* sp. nov. **A.** Right forcipule, dorsal view (CHI108); **B.** Right forcipule, ventral view (CHI108); **C.** Calyx of venom gland (CHI108); **D.** Forcipular coxosternite, ventral view (CHI108); **E.** Left forcipule of juvenile, ventral view (CHI109).

(Fig. 10). Anal pores distinct, opening near the margin of the anal valves (covered by gonopods in male).

Juvenile. Clypeus with conspicuous, uniform reticulation (cells less numerous and larger relative to size of clypeus than in adults), resolving to smaller cells near the medial pair of setae (Fig. 6B). Forcipular trochanteroprefemur approximately as long as wide (Fig. 7E). Anterior metasternites with band of pores posteriorly. Posterior metasternites with pore fields indistinct (Fig. 8C). Last leg-bearing segment coxopleuron with only the one isolated coxal pore present (Fig. 9C). Gonopodal lamina indistinct.

Etymology. Derived from the Latin term for “meager” or “feeble” (“tenuis”), in recognition of its morphological similarity to the initially recognized *G. captiosus* sp. nov. as well as its smaller body size and gracile habitus.

Remarks. *G. tenuis* sp. nov. greatly resembles *G. captiosus* sp. nov. in overall morphology, with many differences between the two species known to be characters that vary with respect to body size in Geophilidae (Homeland and Meidell 2009; Gregory and Barber 2010; Peretti and Bonato 2016; Stojanović et al. 2020). A consistent morphological

difference between the two not subject to allometric scaling is the arrangement of coxal pores, which open at the edges of the ultimate leg-bearing segment metasternite in *G. tenuis* sp. nov. and are scattered over the entire ventrolateral surface of the coxopleuron in *G. captiosus* sp. nov. (Figs 4, 9, 10, Table 1). *G. pusillifrater* overlaps in many morphological characters with *G. tenuis* sp. nov., both being small, oligopodous species (Stojanović et al. 2019). *G. pusillifrater* can be distinguished from *G. tenuis* sp. nov. by the absence of clypeal areas, first maxillary lappets, and carpophagus structures; the earlier mid-body transition in metasternal pore-field shape; the absence of pore fields on the posterior sternites; the lower number of coxal organs; and the sexually dimorphic condition of the male ultimate leg-pair pretarsus, which is reduced to a small tubercle (Lewis 1961; Eason 1964). *G. pygmaeus* similarly resembles *G. tenuis* sp. nov. in size, number of leg-bearing segments, and most other morphological characters (Peretti and Bonato 2016) but clearly differs from it in the elongation of the proximal antennal articles (not elongate), the absence of clypeal areas, the lower number of tubercles on the mid-piece of the

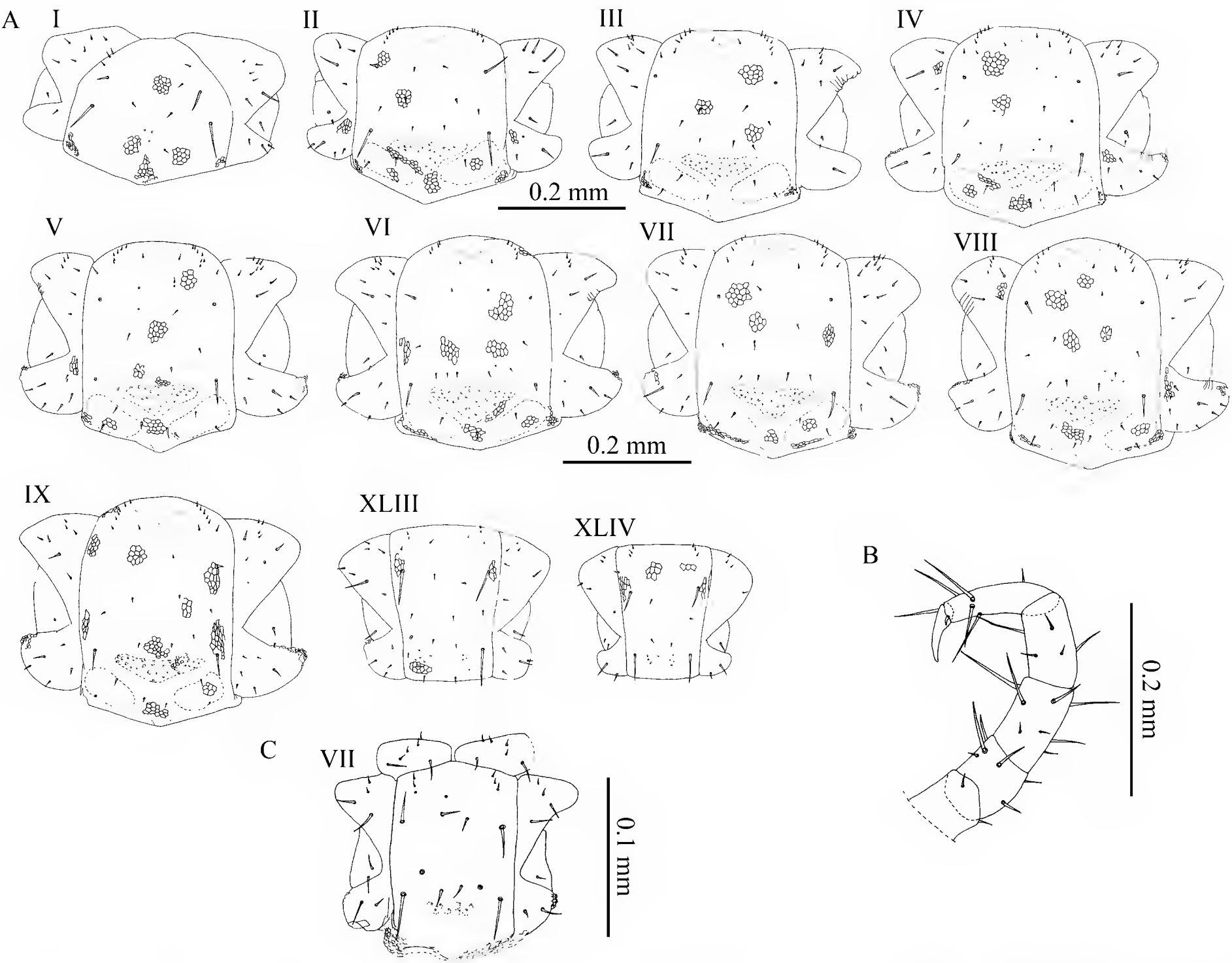


Figure 8. *Geophilus tenuis* sp. nov. **A.** Sternites, ventral view (CHI108); **B.** Walking leg 44, lateral view (CHI108); **C.** Anterior sternite, juvenile, lateral view (CHI109).

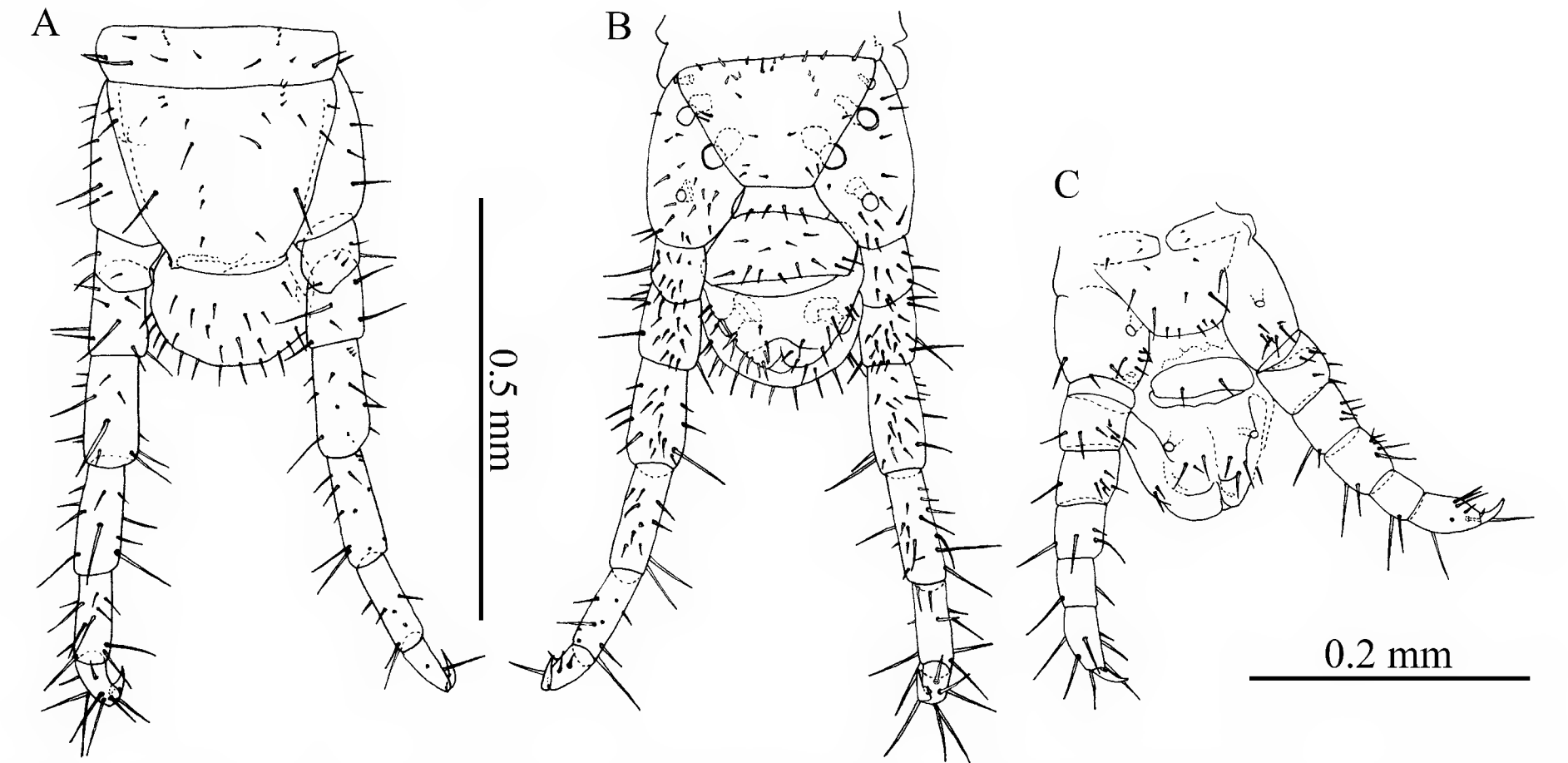


Figure 9. *Geophilus tenuis* sp. nov. **A.** Ultimate leg-bearing segment of female, dorsal view; **B.** Ultimate leg-bearing segment of female, ventral view; **C.** Ultimate leg-bearing segment of juvenile, ventral view (CHI109).

labrum (two), and the arrangement of the coxal organs (one opening at the anterior tip of the coxopleuron, covered by presternites; an isolated coxal organ opening centrally on

the coxopleuron, parallel with the posterior end of the line of coxal organs opening near the edge of the metasternite) (Table 1). Small specimens or juveniles of *G. flavus* may su-

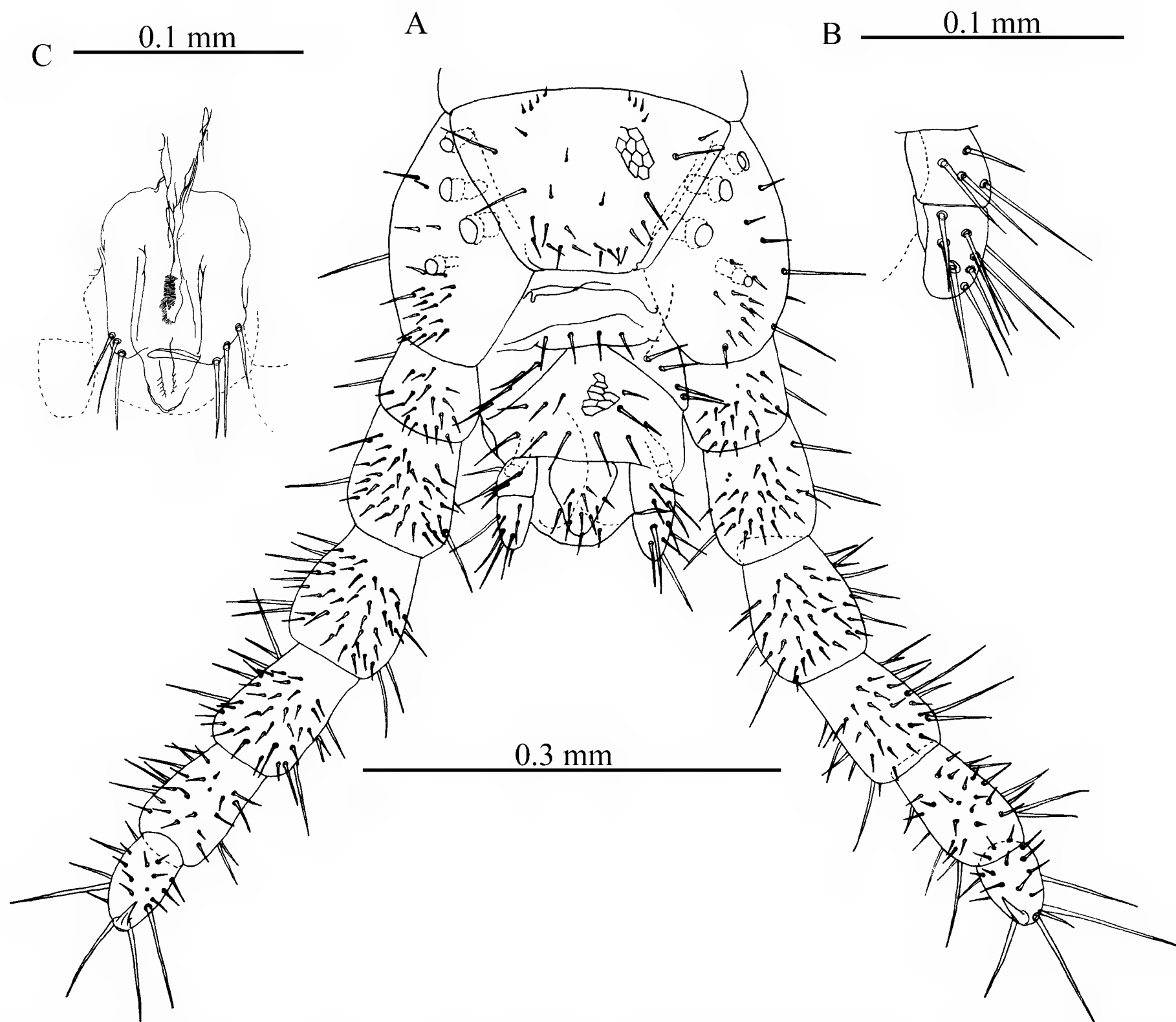


Figure 10. *Geophilus tenuis* sp. nov. **A.** Ultimate leg-bearing segment of male, ventral view (CHI110); **B.** Right male gonopod, ventral view (CHI110); **C.** Penis, ventral view (CHI110).

perficially overlap with *G. tenuis* sp. nov. in meristic or continuous characters that scale allometrically with body size but can be readily distinguished from the new species by the serrate inner edge of the tarsungulum (lacking serrations in *G. tenuis* sp. nov.), the lack of a conspicuous isolated coxal pore (present in *G. tenuis* sp. nov.), and the reduction of the last leg pretarsus (not reduced in size in *G. tenuis* sp. nov.). The species *G. osquidatum*, *G. seurati*, and *G. zagreus* are not known to overlap in adult body length or number of leg-bearing segments with *G. tenuis* sp. nov., but they are additionally distinguished from the new species in having serrations on the inner edge of the tarsungulum (*G. osquidatum*, *G. seurati*), coxal pores that open across the entire ventral surface of the coxopleuron (*G. zagreus*), no isolated coxal pore (*G. osquidatum*, *G. seurati*), and a reduced last leg pretarsus (*G. osquidatum*, *G. seurati*). *G. tenuis* sp. nov. can be distinguished from *G. proximus* by the morphology of the carpophagus structures (strongly sclerotized and consolidated sensu Crabill (1954) in *G. proximus*; unconsolidated sensu Crabill 1954 in *G. tenuis* sp. nov.), the elongation of its forcipules (tarsungula not protruding beyond the anterior margin of the head in *G. proximus*; protruding in *G. tenuis* sp. nov.), the absence of pore fields

on the posterior trunk metasternites (present in *G. tenuis* sp. nov.), and the arrangement of the coxal organs.

Phylogenetic position of *G. captiosus* sp. nov. and *G. tenuis* sp. nov.

Neither maximum likelihood (ML) (Suppl. material 4) nor Bayesian inference (BI) (Fig. 11) analysis recovered the monophyly of *Geophilus*, with the genus found to be paraphyletic with respect to other species of Geophilidae included in the analysis as outgroups (Fig. 11, Suppl. material 4). Both analyses recovered with strong support the monophyly of a group comprising the three morphologically similar species *G. captiosus* sp. nov. (Southern Carpathians), *G. tenuis* sp. nov. (Wallachian Plain), and *G. zagreus* (Dobrogea), all known from adjacent localities in SE Europe (Fig. 12). A clade comprising these three species and *G. flavus* was recovered with moderate support in both analyses. *G. carpophagus* sequences were recovered as a monophyletic clade, occupying the earliest-branching position among the geophilid taxa included in the analysis. All species of *Geophilus* for which multiple sequences were avail-

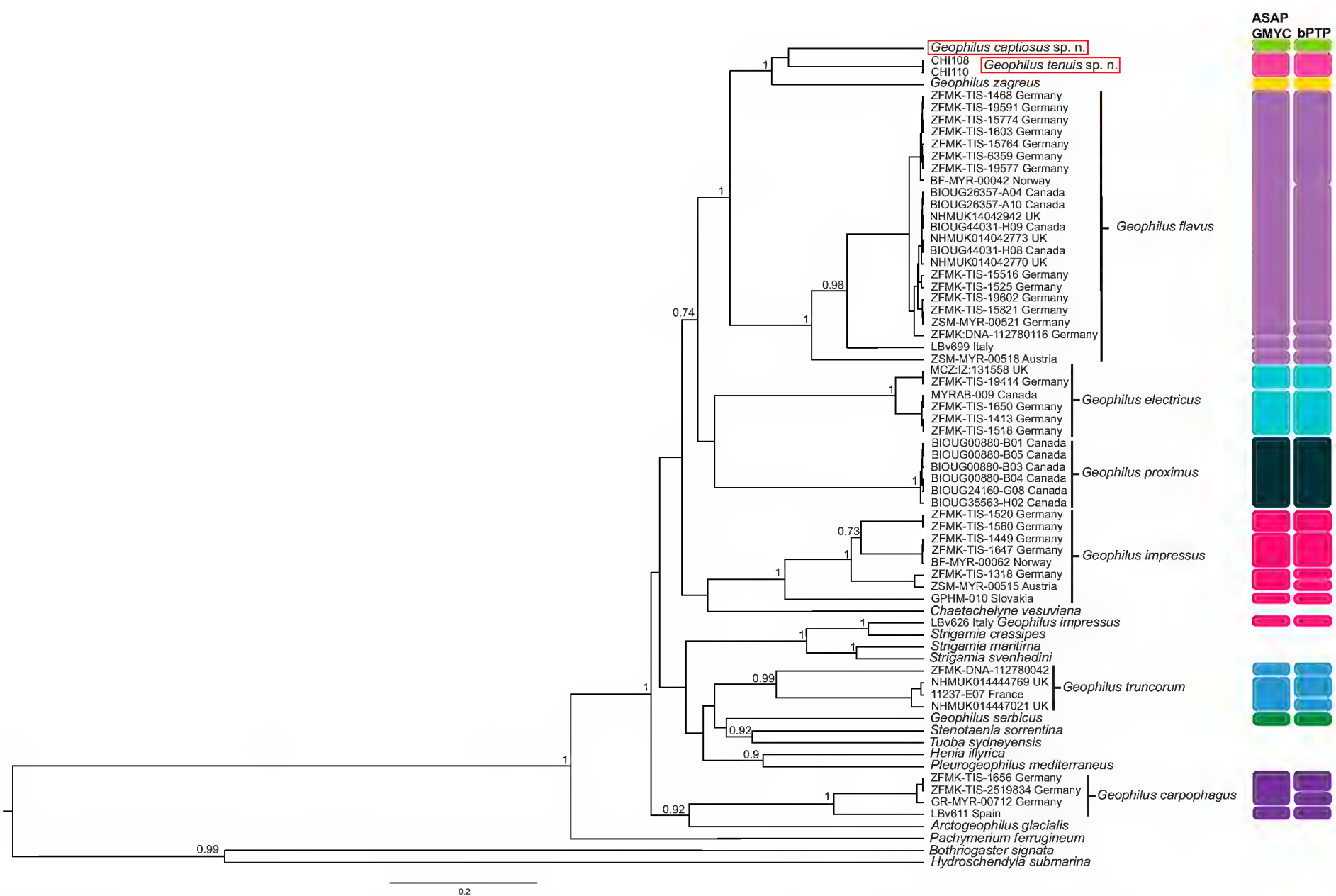


Figure 11. Bayesian inference tree resulting from analysis of full molecular dataset (18S+28S+COI). Nodal support represented by posterior probability values above 0.5 indicated near respective nodes. The new species *Geophilus captiosus* sp. nov. and *Geophilus tenuis* sp. nov. are marked by red boxes. Results of molecular species delimitation analyses based on the COI fragment of *Geophilus* shown. Colors of rectangles correspond to morphological species hypotheses.

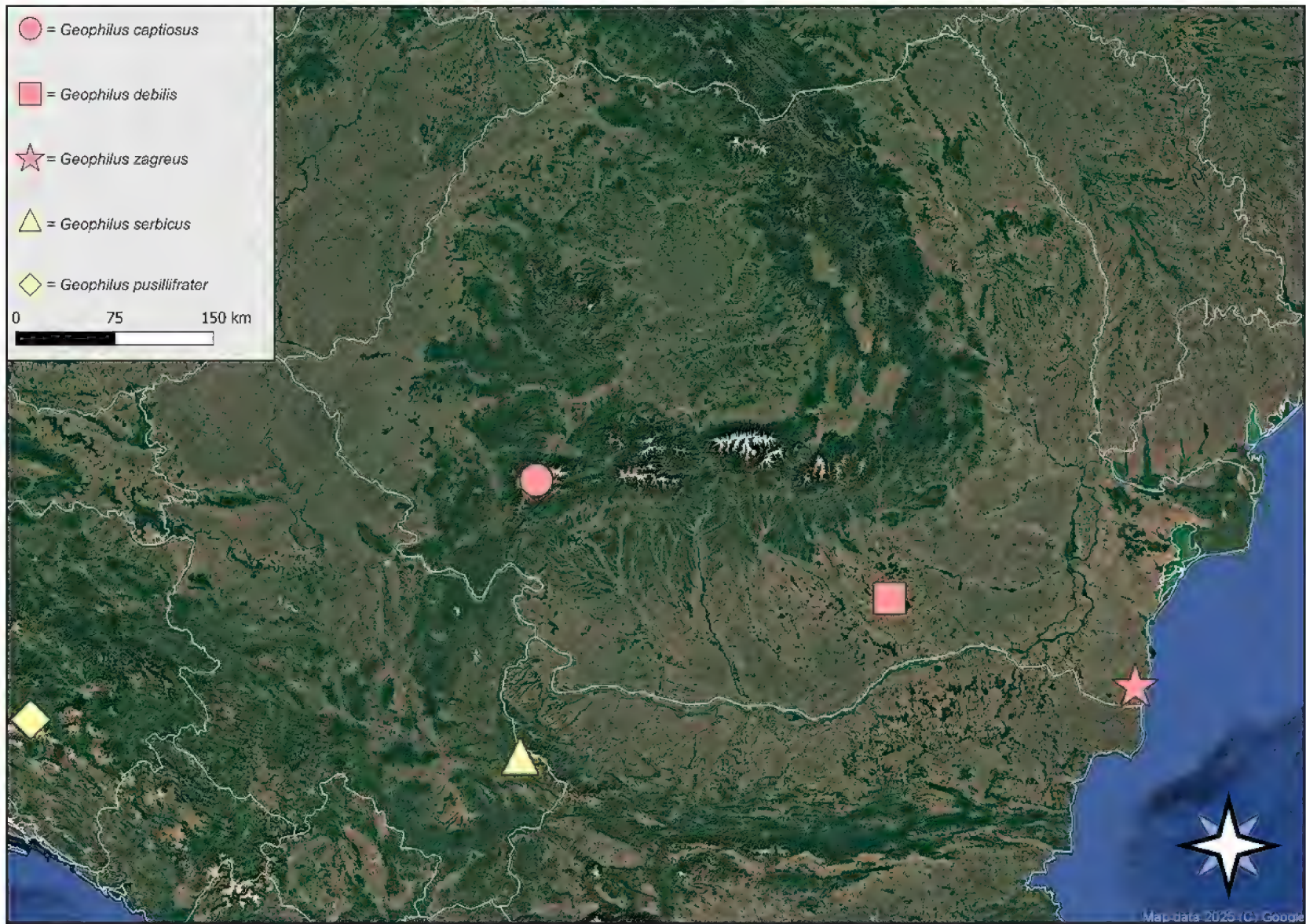


Figure 12. Distribution map of *Geophilus captiosus* sp. nov. and *Geophilus tenuis* sp. nov. and all of the recorded SE-European localities of *G. pusillifrater*, *G. serbicus*, and *G. zagreus*.

able were recovered as reciprocally monophyletic clades, with the exception of *G. impressus* (Fig. 11) in BI analysis.

Across the species of *Geophilus* included in the analysis, only one clade was recovered with strong support in the BI tree (Fig. 11), comprising *G. electricus*, *G. proximus*, *G. flavus*, *G. zagreus*, *G. captiosus* sp. nov. and *G. tenuis* sp. nov. In addition to *G. impressus*, which was found to be paraphyletic with respect to the outgroups in both analyses, all other *Geophilus* species represented by multiple sequences were recovered as monophyletic with strong or unambiguous nodal support.

Molecular diagnosis and species delimitation

All molecular delimitation and diagnosis analyses were carried out on sequences assigned to *Geophilus*, not including any of the other geophilomorph outgroups used in phylogenetic analysis. From the COI data analyzed, 57 of 57 total sequences were read following filtering according to the parameters specified in MOLD. No rDNCs were identified for *G. flavus* or *G. impressus*. For all other *Geophilus* taxa evaluated, three rDNCs in the Folmer region of COI were respectively found to distinguish them from congeners in the present dataset (Table 2).

Of the partitions proposed by ASAP, the three highest-scoring proposed 19, 16, and 10 candidate species,

Table 2. Diagnostic nucleotide combinations in the COI barcode region of *Geophilus* sequences examined.

Species (number of specimens)	Diagnostic nucleotide position			
	A	T	C	G
<i>Geophilus captiosus</i> sp. nov. (1)	-	-	155	29
<i>Geophilus carpophagus</i> (4)	-	-	192, 194	-
<i>Geophilus tenuis</i> sp. nov. (2)	-	26	-	281
<i>Geophilus electricus</i> (6)	-	140	53	-
<i>Geophilus flavus</i> (22)	-	-	-	-
<i>Geophilus impressus</i> (10)	-	-	-	-
<i>Geophilus proximus</i> (6)	-	26	-	281
<i>Geophilus serbicus</i> (1)	-	-	95	85
<i>Geophilus truncorum</i> (4)	41	-	-	465
<i>Geophilus zagreus</i> (1)	-	320	-	248

respectively. The partition with the lowest ASAP-score (Partition 1, 19 candidate species) showed the greatest concordance with the other DNA-based delimitation methods employed. Partition 2 (16 candidate species) more closely matched morphological species hypotheses, only splitting *G. flavus*, *G. impressus*, and *G. truncorum* into more candidate species than suggested by morphological data. Partition 3 (10 candidate species) disagreed with morphological species hypotheses, lumping *G. impressus* and *G. truncorum* into one group. The partition with the lowest ASAP-score is shown in Fig. 11.

GMYC analysis recovered 19 candidate species that were congruent with ASAP partition 1. Differences between ASAP/GMYC and bPTP included the partition of the *G. flavus* clade, with sequences from Norway, Germany, the UK, and Canada, into three candidate species by bPTP but retained as one candidate species by ASAP/GMYC. Similarly, bPTP partitioned the NHMUK014444769 *G. truncorum* sequence into a separate candidate species that was not recovered by ASAP/GMYC. *G. impressus* sequences were partitioned into five concordant candidate species by ASAP and GMYC. bPTP recovered six candidate species within *G. impressus*, splitting a clade comprising sequences from specimens ZFMK-TIS-1318 and ZSM-MYR-00515.

All molecular species delimitation methods identified a larger number of candidate species (19–24) than the number of putative species (10) suggested by identification based on morphology. No complete consensus was found between the different delimitation methods employed; however, across all analyses, candidate species corresponding to *G. captiosus* sp. nov., *G. tenuis* sp. nov., *G. proximus*, *G. serbicus*, and *G. zagreus* matched morphological species hypotheses. Among the remaining nominal species, all methods identified a minimum of five candidate species in *G. impressus*, three within *G. flavus*, and two within *G. truncorum* and *G. carpophagus*.

Uncorrected pairwise distances estimated for the COI barcode in *Geophilus* corroborated the results of molecular species delimitation analyses, with the maximal intraspecific distances observed being 20.8%, 14.1%, 13%,

Table 3. Ranges of uncorrected pairwise distances (%) based on the COI barcode region within and between *Geophilus* species analyzed. Number of individuals and associated sequences in brackets.

Species	<i>Geophilus captiosus</i> sp. nov.	<i>Geophilus tenuis</i> sp. nov.	<i>Geophilus carpophagus</i>	<i>Geophilus electricus</i>	<i>Geophilus flavus</i>	<i>Geophilus impressus</i>	<i>Geophilus proximus</i>	<i>Geophilus serbicus</i>	<i>Geophilus truncorum</i>	<i>Geophilus zagreus</i>
<i>G. captiosus</i> sp. nov. (1)	NA									
<i>G. tenuis</i> sp. nov. (2)	16.2	0								
<i>G. carpophagus</i> (4)	18.9–19.1	19.7–20.1	0–10.9							
<i>G. electricus</i> (6)	19.9–20.2	19.5–20.9	17.2–19	0–4.9						
<i>G. flavus</i>	16.1–17.4	17.2–18.3	16.4–19.8	17.3–19.5	0–13					
<i>G. impressus</i> (9)	16.7–19.3	18.1–20.7	16.4–21	16.8–19.8	18.1–21	0–20.8				
<i>G. proximus</i> (7)	18.3–18.4	21.3–21.8	18.9–20.5	19.1–20.2	17–19	18.1–21	0–0.3			
<i>G. serbicus</i> (1)	19.6	23.9	18.5–19.9	20.1–21	18.1–18.7	18.2–20.5	18.7–19	NA		
<i>G. truncorum</i> (4)	18.1–19.5	20.9 – 22.2	16.4–19	16.3–20.2	16.1–18.1	14.8–20.6	17.5–17.8	15.6–16.1	0.3–14.1	
<i>G. zagreus</i> (1)	17.4	16.9	17.8–19.1	15.4–17.1	17–18.3	17.6–19.4	17.1	20.2	15.9–16.5	NA

10.9%, and 4.9% among sequences assigned to *G. impressus*, *G. truncorum*, *G. flavus*, *G. carpophagus*, and *G. electricus*, respectively (Table 3, Suppl. material 2). Both *G. captiosus* sp. nov. and *G. tenuis* sp. nov. exhibit more than 16.1% distance from all other sequences in the dataset, with the lowest interspecific distance (16.1%) being observed between *G. captiosus* sp. nov. and *G. flavus* (Table 3, Suppl. material 2).

Discussion

Affinities and intraspecific variation in European *Geophilus*

The two species here described are retrieved by both phylogenetic reconstruction and genetic distance comparisons (Fig. 11, Table 3, Suppl. material 4) as closely allied to *G. flavus* and *G. zagreus*, forming a monophyletic clade with these taxa. These results support the inferred similarity between these taxa based on diagnostic morphological characters. All species belonging to this clade show elongation of the cephalic capsule and antennal articles, the presence of paired clypeal areas, and the presence of two pairs of maxillary lappets. Furthermore, *G. captiosus* sp. nov., *G. tenuis* sp. nov., and *G. zagreus* form a strongly supported clade despite the geographic isolation and habitat differences between the type localities of these taxa. Each is only known from the Southern Carpathians, Wallachian Plain, and Dobrogean karst, respectively (Fig. 12). Both *G. captiosus* sp. nov. and *G. tenuis* sp. nov. were found near the soil surface in their respective localities (see below), contrasting with the troglobite *G. zagreus*, which is not known from any surface sites in Dobrogea (Baba et al. 2024). Phylogenetic analysis does not recover the geographically proximate and morphologically similar *G. serbicus* in the same clade as the new species described from Romania, which are closely related to the troglobiont *G. zagreus*. Preliminary molecular phylogenetic analysis of the new species here described thus tentatively indicates possible convergence on small-sized oligopodous ecomorphs in SE-European *Geophilus* species.

G. flavus, although retrieved as monophyletic in our analyses, shows high genetic variability, and at least three lineages are consistently recovered within it, with significant branch length. This is supported by MOLD analysis, which failed to recover rDNCs in the *G. flavus* COI barcode region for the present dataset. Previous morphological variation in Austrian *G. flavus* populations has been interpreted to represent subspecies or varieties of the nominal form, which show continuous variation in morphological characters frequently interpreted as taxonomically significant in *Geophilus* (structure of the clypeal areas, body size, number of leg-bearing segments, and number of coxal organs) (Christian 1996). Notably, specimens from the historical regions of Bohemia, Moravia, and Silesia and some Austrian localities described as “*Geo-*

philus longicornis var. *austriacus*” Latzel, 1880 overlap in number of leg-bearing segments (43–49), coxal organs (1–5), and structure of the clypeal areas (paired, separated, marked by reduced reticulation) with both *G. captiosus* sp. nov. and *G. tenuis* sp. nov. However, all *G. flavus* specimens examined by Christian (1996), including the nominal varieties that superficially resemble *G. captiosus* sp. nov. and *G. tenuis* sp. nov., consistently differ from the two new species here described in the chaetotaxy of the forcipular coxosternite (three macrosetae arranged in an inverted triangle pattern in *G. flavus*; no such arrangement in *G. captiosus* sp. nov. and *G. tenuis* sp. nov.) and the anterior walking legs (distinct, long macroseta present on the intermediate articles of the anterior walking legs in *G. flavus*; no distinct macroseta in *G. captiosus* sp. nov. and *G. tenuis* sp. nov.) and in the absence of an isolated coxal pore on the last-leg-bearing segment coxopleuron (present in *G. captiosus* sp. nov. and *G. tenuis* sp. nov.). Additional sampling of Central European *G. flavus* is needed to conclusively establish the range of morphological variation in this likely species complex.

The identity of the morphologically divergent Austrian populations has been nominally maintained as *G. flavus* (Christian 1996) and is consistent with known ontogenetic variation in this species (Popovici 2024), but the variation observed in species delimitation analyses, phylogenetic reconstruction, and morphological characters across *G. flavus* in Central Europe indicates the presence of extensive population structure and possibly a cryptic species complex. Integrative taxonomy of these divergent populations and sampling additional individuals across its range are needed to clarify the taxonomic uncertainty surrounding Central European *G. flavus*.

Variation in the presence and conspicuousness of clypeal areas is also recorded here in *G. seurati*, with the three Algerian specimens examined showing evident paired clypeal areas (Table 1), contrasting with specimens nominally assigned to *G. seurati* from the UK in which clypeal areas are recorded as absent (Lewis 1962). Similar variability in the shape and extent of the clypeal area has also been recorded in *G. proximus* (Barber and Jones 1999; Thénard et al. 2024).

In addition to *G. flavus*, *G. impressus* also showed significant variability in sequence data, consistent with ranges of interspecific variability across the other *Geophilus* species here included in molecular species delimitation analyses. No rDNCs were identified for either species (Table 2), and all molecular species delimitation tools partitioned sequences assigned to either of the two into 3–6 candidate species. Although the sampling included in these analyses is far from representative of the range of either species, these results, indicating higher genetic variability than expected intraspecifically, suggest *G. flavus* and *G. impressus* (Table 3, Suppl. material 2) are likely cryptic species complexes within *Geophilus* and in need of taxonomic revision.

The populations sampled under the name *G. truncorum* seem to belong to at least three different species. These

were recovered by all three species delimitation methods (Fig. 11). The same situation is found in *G. impressus*, where the analyzed populations are part of a species complex that would unite at least five candidate species under the current proposed identification of sequences retrieved from public repositories.

Although not systematically reviewed, the association of certain characters (number of leg-bearing segments and coxal organs, presence of unconsolidated carpophagus structures, separation of the clypeal areas) with reduced body size in *Geophilus* could indicate that similarities between *G. serbicus* and Austrian *G. flavus* to endemic Romanian taxa reflect convergence due to miniaturization.

Biogeographic notes

Both new species here described have been hitherto only collected in their respective type localities. These are characterized by different vegetation assemblages and altitudes. *G. captiosus* sp. nov. has been collected in Carpathian mixed beech and fir forest (vegetation unit F₉₂ in Doniță et al. (1992), characterized by *Abies alba*, *Fagus sylvatica* tree cover, and *Aremonia agrimonoides*, *Dentaria glandulosa*, *Pulmonaria rubra*, *Ranunculus carpathicus*, and *Symphytum cordatum* undergrowth) at alt. 1086 m. *G. tenuis* sp. nov. has been collected in xerothermophilus oak forest (vegetation unit G_{17a} in Doniță et al. (1992), characterized by *Carpinus orientalis*, *Quercus cerris*, *Quercus pedunculiflora*, *Quercus pubescens*, *Tilia tomentosa* tree cover, and *Allium ursinum*, *Arum italicum*, *Cormus domestica*, and *Rubus tomentosus* undergrowth) at alt. 90–100 m.

Both species were recorded from leaf litter, under stones, and inside rotten wood, as well as within the upper soil layers. Although based on limited sampling, this spatial distribution closely resembles that described for *G. impressus* in Northwest Romanian deciduous forests (Gava 2009) and contrasts with syntopic *G. electricus*, which is only recorded from within the soil, below associated surface microhabitats (Gava 2009).

Absence from nearby localities likely reflects the lack of sufficiently intensive sampling of Geophilomorpha even in areas considered to be hotspots of sampling effort. The type locality of *G. captiosus* sp. nov. is considered among the most intensively sampled sites with respect to centipedes in Romania (Baba et al. 2019).

In addition to *G. serbicus*, the only other *Geophilus* species characterized by a small body size, claw-shaped second maxillary pretarsus, and fewer than 47 leg-bearing segments described from Southeastern Europe is *G. pusillifrater* (Fig. 12). Whether *G. captiosus* sp. nov. and *G. tenuis* sp. nov. can be adequately characterized as microendemic lineages belonging to a widespread group of small *Geophilus* in Southeastern Europe and the Balkan Peninsula can only be resolved pending revision of the taxonomic status of similar species described in past literature, as well as a systematic survey of suitable microhabitats in order to gain more complete information on their distribution. Notably,

G. pusillifrater, originally described from Bosnia and Herzegovina, greatly resembles the morphology of *G. tenuis* sp. nov., but its affinity to this species cannot be conclusively established in the absence of molecular data and recent taxonomic re-evaluation of the status of SE European *G. pusillifrater* populations. The morphologically similar *G. pygmaeus* has only been recorded in Central Europe, with its only published Carpathian records being uncertain and restricted to Slovakia, and the apparent southern limit of its distribution being represented by Slovenian records from the Northern Dinaric Alps (Peretti and Bonato 2016). Patchy distribution data for geophilomorph species in Southeastern Europe represents a major challenge for clarifying the status of poorly known taxa and interrogating the emerging biogeographical patterns that highlight this region as a hotspot of *Geophilus* species diversity.

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Supplementary material 1

Sequence information and associated metadata for the molecular dataset

Authors: George Popovici, Oana Paula Popa, Elena Iulia Iorgu

Data type: xlsx

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Supplementary material 2

Uncorrected p-distances across evaluated COI gene sequences of *Geophilus*

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Data type: xlsx

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Supplementary material 3

Occurrence data for accessioned specimens of the two new species described in Darwin Core format

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Data type: xlsx

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Supplementary material 4

Maximum likelihood tree resulting from analysis of full molecular dataset (18S+28S+COI)

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Data type: pdf

Explanation note: Maximum likelihood tree resulting from analysis of full molecular dataset (18S+28S+COI) with $\ln L = -17673.869$. Nodal support represented by UF-Boot values above 50 indicated near respective nodes. The new species *Geophilus captiosus* sp. nov. and *Geophilus tenuis* sp. nov. are marked by red boxes.

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